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Interrelationships of Polydolopidae (Mammalia: Marsupialia) from South America and Antarctica

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Polydolopidae is a family of Palaeogene marsupials recorded from outcrops in southern South America and the Antarctic Peninsula. They are mostly represented by skull fragments or maxillary, dentary and molar remains. A taxonomic and systematic revision is carried out with the inclusion of a phylogenetic analysis encompassing almost every polydolopid species and five marsupial species found to be related to them in previous analyses (*Bonapartherium hinakusijum*, *Epidolops ameghinoi*, *Microbiotherium tehuelchum*, *Prepidolops didelphoides* and *Roberthoffstetteria nationalgeographica*). The Polydolopidae was recovered as a monophyletic group, even though no resolution about its sister-group can be found. The following genera are recovered: *Antarctodolops*, *Amphidolops*, *Archaeodolops*, *Eudolops*, ***Hypodolops* gen. nov.**, *Kramadolops*, *Pliodolops*, *Pseudolops* and two unidentified genera (Gen. et sp. indet 1 and 2). One genus and three new species are recognized. The family appeared at the beginning of the Palaeocene and disappeared during the Early Oligocene. The extinction of the group could be related to climatic deterioration in the Early Oligocene, when temperature and the humidity dropped, provoking desertification in the region where Polydolopids evolved.

ADDITIONAL KEYWORDS: Caenozoic – Metatheria – Palaeogene – sytematics.

INTRODUCTION

Polydolopidae comprises a group of Palaeogene marsupials that, except for the Antarctic forms, have an exclusive South American distribution, being found in southern Argentina and central Chile (Fig. 1). Their biochron span from the Early Palaeocene to the Early Oligocene (Goin *et al.*, 2010; Krause *et al.*, 2017; Fig. 2). In Argentinean Patagonia, localities with Polydolopids are mostly restricted to the centre and east of Chubut Province (Figs 1, 2), where the Río Chico Group and the Sarmiento Formation crop out. West of the Chubut Province are the Tufolitas Laguna del Hunco and Andesitas Huancache formations, where the Paso del Sapo fauna was exhumed (Tejedor *et al.*, 2009). In the last decade, several stratigraphic and geochronologic analyses were carried out on the Río Chico Group (e.g. Ré *et al.*, 2010a, b; Dunn *et al.*, 2013; Clyde *et al.*, 2014; Woodburne *et al.*, 2014a, b; Krause *et al.*, 2017) in the Sarmiento Formation (e.g. Madden *et al.*, 2005; Ré *et al.*, 2005, 2010a, b) and also in the La Meseta Formation at the Marambio (Seymour) Island of the Antarctic Peninsula (Reguero *et al.*, 2002; Montes *et al.*, 2013). A summary of the localities with polydolopids is shown in Figure 1 and Table 1. A present-day biostratigraphy and biochronology is shown in Figure 2.

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HISTORY OF THE FAMILY, GENERA AND SPECIES OF POLYDOLOPIDAE

Originally, Ameghino (1897) assigned Polydolopidae to the suborder Multituberculata of the order Plagiaulacoidea (Ameghino, 1889). Later, he considered that polydolopids derived from the caenolestids 'Garzoniidae' (Caenolestinae *sensu* Marshall, 1980) and that these gave origin to 'Abderitidae' (Abderitinae *sensu* Marhall, 1980). Gregory (1910) considered the similarities among polydolopids and multituberculates as convergent and

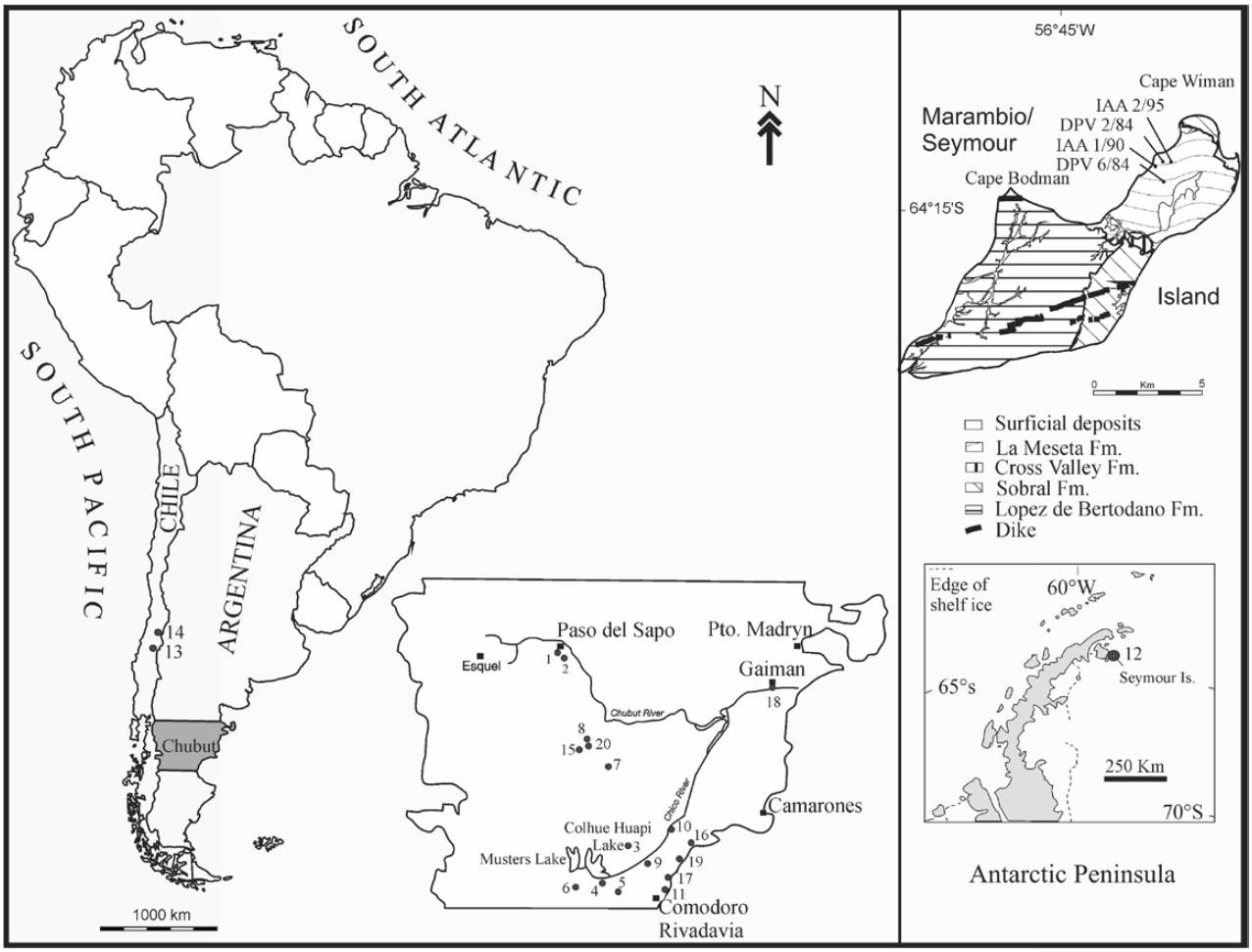

Figure 1. Map of South America and Antarctic Peninsula showing the localities with published Polydolopiformes. Localities: 1, Laguna Fria; 2, La Barda; 3, Cañadón Vaca; 4, Gran Barranca (Includes La Cancha, la Cantera and Las Flores localities); 5, Southern Cliff of Valle Hermoso; 6, Cerro Blanco; 7, Rinconada de los López; 8, Laguna de la Bombilla; 9, Cañadón Hondo; 10, Cabeza Blanca; 11, Bahía Solano; 12, Marambio/Seymour Island; 13, Termas del Flaco; 14, Cachapoal Valley; 15, La Gran Hondonada; 16, Cerro Redondo; 17, Bajo de la Palangana; 18, Gaiman; 19, Lomas Blancas; 20, Cerro Conhué.

regarded Polydolopidae as a specialized branch of the caenolestoids (Paucituberculata; see: Marshall, 1980). Even though the marsupial nature of polydolopids was then generally accepted (e.g. Simpson, 1928, 1935a, b; Marshall, 1982; Goin *et al.*, 2003; Flynn & Wyss, 2004), the interpretation about their affinities has been questioned (e.g. Aplin & Archer, 1987; Rangel *et al.*, 2019) and are still controversial. Simpson (1928) considered polydolopids as a group closely related to Caenolestidae. Archer (1984) and subsequent authors considered Polydolopidae as part of the Polydolopimorphia (Goin *et al.*, 2016).

Pascual & Bond (1981) considered *Polydolops* Ameghino, 1897 and allies as closely related to *Epidolops* Paula Couto, 1952, from the Early Eocene Itaboraí Formation, Brazil, thus recognizing two subfamilies among Polydolopidae: Epidolopinae (only represented by *Epidolops*) and Polydolopinae (*Polydolops* and allies, from the Palaeogene of Patagonia). Goin *et al.*, (2003) considered that only Polydolopinae was included in Polydolopidae, and that they were more closely related to *Roberthoffstetteria nationalgeographica* Marshall *et al.*, 1983, formerly regarded as a caroloameghinid, from the Palaeocene of Bolivia (Marshall *et al.*, 1983).

Considering the systematic arrangements in Marshall *et al.* (1990), Flynn & Wyss (1999) redefined the order Polydolopimorphia and the groups within using the nomination and conventions proposed by de Queiroz & Gauthier (1990, 1992 *fide* Flynn & Wyss, 1999). They defined Polydolopimorphia as the group composed of all marsupials more closely related to Polydolopoidea than to any other marsupial, living or extinct. Subsequently, they defined Polydolopoidea as

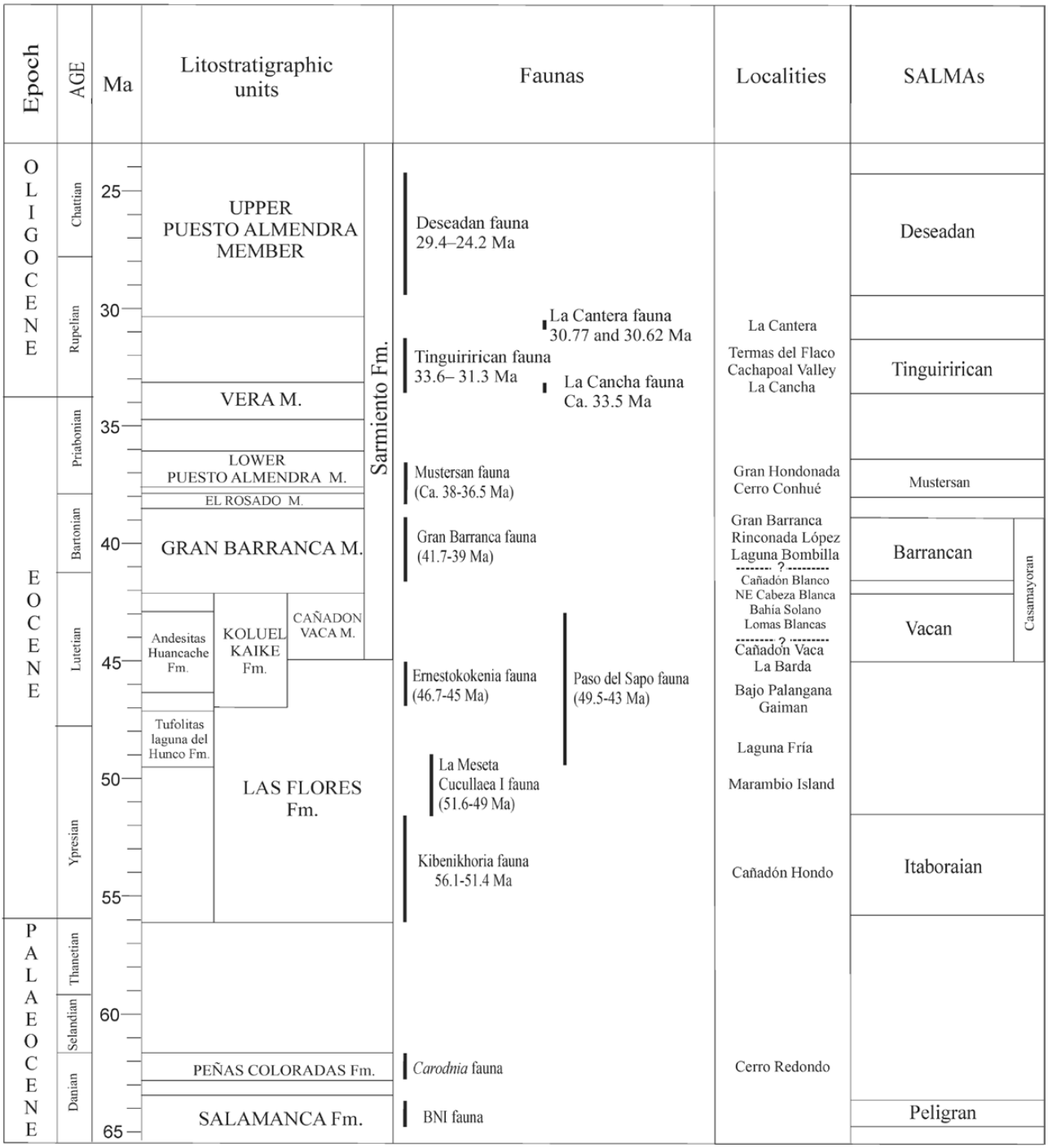

Figure 2. Palaeogene timescale showing litostratigraphic units from Argentinean Patagonia, South American and Antarctic faunas, localities with polydolopids and SALMAs. Age and Epoch follow Cohen *et al.* (2013; updated 2020). Palaeogene units follow Tejedor *et al.* (2009), Ré *et al.* (2010a, b), Dunn *et al.* (2013), Clyde *et al.* (2014); Comer *et al.* (2015), Krause *et al.* (2017), Flynn *et al.* (2003), Montes *et al.* (2013) and Zimicz *et al.* (2020).

the clade including the most recent common ancestor of *Prepidolops* Pacual, 1980 and Polydolopiformes and all their descendants (considered later Polydolopimorphia; e.g. Goin *et al.*, 2016). Polydolopiformes is the clade comprising the most recent common ancestor of *Bonapartherium* Pacual, 1980 and Polydolopidae plus all their descendants. Finally, Polydolopidae was characterized as the group that includes the most

Table 1. Localities with Polydolopidae. The units correspond to the ones from which polydolopid specimens were recovered

Locality	Geographic location	Salma/fauna	Age	Geologic unit	Main reference
Cerro Redondo	Chubut, Argentina	*Carodnia* fauna	Late Danian	Peñas Coloradas Fm.	Simpson, 1935b
Cañadón Hondo	Chubut, Argentina	Itaboraian	Early Eocene	Las Flores Fm. (lower part)	Simpson, 1935b; Krause *et al.*, 2017
Marambio/Seymour Island	Antarctic Peninsula, Argentina	La Meseta fauna	Early Eocene	La Meseta Formation (*Cucullaea I* Allomember)	Marenssi *et al.*, 1998; Montes *et al.*, 2013
Bajo de la Palangana	Chubut, Argentina	*Ernestokokenia* fauna	Middle Eocene	Las Flores Fm. (upper part)	Simpson, 1935b; Krause *et al.*, 2017
Gaiman	Chubut, Argentina	*Ernestokokenia* fauna	Middle Eocene	Las Flores Fm. (upper part)	Simpson, 1935b; Krause *et al.*, 2017
Laguna Fría	Chubut, Argentina	Paso del Sapo fauna	Middle Eocene	Tufolitas Laguna del Hunco	Tejedor *et al.*, 2009
La Barda	Chubut, Argentina	Paso del Sapo fauna	Middle Eocene	Andesitas Huancache Formation	Tejedor *et al.*, 2009
Cañadón Vaca	Chubut, Argentina	Vacan	Middle Eocene	Sarmiento Fm. (Vacan Member)	Cifelli, 1985; Ré *et al.*, 2010a, b
Laguna de la Bombilla (and near localities)	Chubut, Argentina	Barrancan	Middle Eocene	Sarmiento Fm. (Gran Barranca Member)	Marshall, 1982; Ré *et al.*, 2010a, b
Gran Barranca	Chubut, Argentina	Barrancan	Middle Eocene	Sarmiento Fm. (Gran Barranca Member)	Ré *et al.*, 2010a, b
Southern slope from Valle Hermoso	Chubut, Argentina	Barrancan	Middle Eocene	Sarmiento Fm. (Gran Barranca Member)	Goin & Candela, 1998; Ré *et al.*, 2010a, b
Rinconada de los López	Chubut, Argentina	Barrancan	Middle Eocene	Sarmiento Fm. (Gran Barranca Member)	Cifelli, 1985
Cerro Blanco	Chubut, Argentina	Casamayoran	Middle Eocene	Sarmiento Fm. (Probably Gran Barranca Member)	Simpson, 1948
NE from Cabeza Blanca	Chubut, Argentina	Casamayoran	Middle Eocene	Sarmiento Fm.	Reguero & Escribano, 1996; Lema *et al.*, 2001
Bahía Solano	Chubut, Argentina	Casamayoran	Middle Eocene	Sarmiento Fm.	Marshall, 1982
Lomas Blancas	Chubut, Argentina	Casamayoran	Middle Eocene	Sarmiento Fm.	Reguero 1999; Marshall, 1982
Cerro Conhué	Chubut, Argentina	Mustersan	Late Eocene	Sarmiento Fm.	Marshall, 1982
La Gran Hondonada	Chubut, Argentina	Mustersan	Late Eocene	Sarmiento Fm. (lower Puesto Almendra M.)	Odreman Rivas, 1978
Locality C-89-39, Termas del Flaco	Central Chile	Tinguiririan	Early Oligocene	Abanico Fm.	Flynn *et al.*, 2003

Table 1. Continued

Locality	Geographic location	Salma/fauna	Age	Geologic unit	Main reference
Cahcapoal Valley	Central Chile	Tinguiririca	Early Oligocene	Abanico Fm.	Flynn *et al.*, 2003
La Cancha	Chubut, Argentina	Tinguiririca	Early Oligocene	Sarmiento Fm. (Vera Member)	Ré *et al.*, 2010a, b; Goin *et al.*, 2010
La Cantera	Chubut, Argentina	La Cantera fauna	Early Oligocene	Sarmiento Fm. (Puesto Almendra Member)	Ré *et al.*, 2010a, b; Dunn *et al.*, 2013

recent common ancestor of *Epidolops* and *Polydolops* plus all their descendants, and Polydolopinae the one including the most recent common ancestor of *Eudolops* and *Polydolops* plus all their descendants (Flynn & Wyss, 1999). This interpretation of Polydolopidae was challenged by Goin *et al.* (2006). They performed the first cladistic analysis including both *Polydolops* and *Epidolops*. Even though the goal of that work was to know the relationships of *Cocatherium lefipanum* Goin *et al.*, 2006 (Early Palaeocene, Chubut Province, Argentina) and the analysis had constraints, the results showed that *Epidolops* was more closely related to *Bonapartherium* than to *Polydolops*. These results were corrected by an analysis carried out by Goin *et al.* (2009) in which *Polydolops* was found to be more closely related to *Roberthoffstetteria* Marshall *et al.*, 1983 (thus both constituting the Polydolopiformes) than to any other marsupial, and *Epidolops* was sister to *Bonapartherium* and *Prepidolops* among other bonapartheriids (this was supported by following analyses; e.g. Chornogubsky & Goin, 2015; Rangel *et al.*, 2018).

When Ameghino (1897) first recognized the family Polydolopidae, he included two species in it: *Eudolops tetragonus* Ameghino, 1897 and *Polydolops thomasi* Ameghino, 1897. He published them as part of his *Faune Pyrotheréen*, but later recognized them as pertaining to his '*Couches à Notostylops*' (Casamayoran SALMA; Middle–Late Eocene; e.g. Ameghino, 1902; Marshall, 1982) from southern Argentina and only represented then by upper dentition. Some years later, Ameghino (1902) recognized a new species of *Polydolops* and three new genera, *Amphidolops*, *Pliodolops*, and *Pseudolops*, all of them pertaining to Polydolopidae. Both *Pliodolops* and *Pseudolops* were monospecific genera. Two species were included in Ameghino's new genus *Amphidolops*: *A. serrifer* Ameghino, 1902 and *A. serrula* Ameghino, 1902. The species of *Polydolops* were considered extremely similar, being differentiated mostly by their size, except for '*Polydolops*' *clavulus* Ameghino, 1902, which is less cuspidate and has a p3 with fewer serrations on its margin (Ameghino, 1902). The species *Promysops* acuminatus Ameghino, 1902, *Propolymastodon cardatus* Ameghino, 1903 and *Propolymastodon caroliameghinoi* Ameghino, 1903 were considered part of the same family, the Promysopidae, which was first considered as part of Rodentia but later moved to Allotheria, deriving from polydolopids, and giving origin to some rodents (Ameghino, 1903). On the other hand, *Anadolops thylacoleoides* Ameghino, 1904, *Orthodolops sciurinus* Ameghino, 1904 and *Polydolops simplex* Ameghino, 1904 were considered as pertaining to Polydolopidae (Ameghino, 1903). Ameghino (1903) also re-evaluated the affinities of '*Polydolops*' *clavulus*

and he created *Archaeodolops* Ameghino, 1904 to include it. He argued that the features of this species (e.g. less crenulated p3, molars with fewer cusps) were primitive, although he considered *A. clavulus* as the ancestor of all other polydolopids. He also reassessed the affinities of '*Amphidolops*' *serrifer*, creating the genus *Anissodolops* Ameghino, 1904 to include that species but he not explain this new assignation.

All species described by Ameghino, when the provenance was provided, come from his 'Couches a *Notostylops*' (Ameghino, 1902). In 1904, Ameghino redefined all new species recognized by him in 1903 (but see the International Code of Zoological Nomenclautre: Art. 12.2.7; Marshall, 1982).

A few decades later, Simpson (1935b) described three polydolopid species from his 'Riochican' SALMA: *?Polydolops kamektsen* Simpson, 1935, *Polydolops winecage* Simpson, 1935 and *Seumadia yapa* Simpson, 1935, followed by *Polydolops rothi* Simpson, 1936. However, none of these come from levels of the same age, *Seumadia yapa* being the oldest polydolopid so far known (early Palaeocene; *Carodnia* faunal zone of Simpson, 1935b). Later, Simpson (1948) revised the family Polydolopidae and only recognized four genera: *Amphidolops*, *Eudolops*, *Polydolops* and *Seumadia*. On the other hand, he subdivided *Polydolops thomasi* into four subspecies based on small differences. Marshall (1982) synonymized the four subspecies of Simpson (1948), included the Late Eocene species *Polydolops mayoi* Odreman Rivas, 1978 and described the new species *Eudolops hernandezi* Marshall, 1982.

After Marshall's revision, the first extra-Patagonian remains were described (Woodburne & Zinsmeister, 1982, 1984; Case *et al.*, 1988): *Antarctodolops dailyi* Woodburne & Zinsmeister, 1984 and *Eurydolops seymourensis* Case *et al.*, 1988, both found in Early Eocene strata from the Antarctic Peninsula. These species were considered as *Polydolops* by Goin & Candela (1995), but synonymized and recognized as *Antarctodolops* by Chornogubsky *et al.* (2009), who also described an additional species, *A. mesetaense* Chornogubsky, Goin & Reguero, 2009.

The most complete remains of this group came from the Early Oligocene of Chile, from where two species were described: *Polydolops abanicoi* Flynn & Wyss, 1999 and *P. mckennai* Flynn & Wyss, 2004. The latter corresponds to the only known skull of a polydolopid. Goin *et al.* (2010) described two new species that were considered related to the ones from Chile, thus reuniting all of them plus *P. mayoi* in the new genus *Kramadolops* Goin *et al.*, 2010. One of the species, *K. maximus* Goin *et al.*, 2010, corresponds to the youngest species of a polydolopid described so far, being exhumed from Early Oligocene strata from La Cantera, Chubut Province. Tejedor *et al.* (2009) described the fauna from the Eocene strata of Paso del Sapo, Chubut Province, from where a new species was proposed (*Polydolops unicus* Tejedor *et al.*, 2009) and several unnamed taxa were briefly described.

The main goal of this paper is to present a new revision and the first extensive phylogenetic analysis of the family Polydolopidae in order to test these previous hypotheses of relationships.

MATERIAL AND METHODS

Studied Material

All known specimens of Polydolopidae, as well as species compared with them or those conforming the outgroup, were observed first-hand, except for specimens FMNH P14717 (*Polydolops thomasi*), SGOPV 2941 (*Kramadolops abanicoi*), UCR 20910 (*Antarctodolops dailyi*) and AMNH 27893 (*Pliodolops winecage*), which were studied from casts and photographs.

Geochronologic and biochronologic framework

Age and epochs follow Cohen *et al.* (2013; updated 2020). The age of the Salamanca Formation follows Clyde *et al.* (2014) and Comer *et al.* (2015); Riochican Group, faunas, and SALMAs follow Simpson (1935a, b) and Bond *et al.* (1995) with observations and modifications from Krause *et al.* (2017) and Zimicz *et al.* (2020). Vacan, Barrancan, Mustersan and Tinguiririan SALMAs with their faunas follow Ré *et al.* (2010a, b) and Dunn *et al.* (2013) for Argentina, and Tinguiririan SALMA follows Flynn *et al.* (2003) for outcrops from Chile. The age of *Cucullaea* I Allomember from La Meseta Formation (Antarctic Peninsula) follows Montes *et al.* (2013) (Fig. 2).

Phylogenetic analysis

For the phylogenetic analysis, a matrix with 25 taxa and 48 characters was used (Supporting Information, Appendices S1, S2). All characters were treated as non-additive. Bremer supports, consistency index (Ci) and retention index (Ri) were calculated. The analysis was carried out using *Tree analysis using New Technology* (TNT) software (Goloboff & Catalano, 2016).

Abbreviations

Institutional abbreviations. AMNH, American Museum of Natural History, Nueva York, USA; FMNH, Field Museum of Natural History, Chicago, USA; LIEB-PV, Vertebrate Paleontology Collection. Laboratorio de Investigaciones en Evolución y Biodiversidad, Universidad Nacional de la Patagonia 'San Juan

Bosco', Sede Esquel, Chubut Province, Argentina; MACN-A, Ameghino Collection. Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MACN-Pv, Museo Collection. Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MLP, División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina; MPEF, Museo Paleontológico Egidio Feruglio Collection, Trelew, Chubut Province, Argentina; SGOPV, Colección Paleontología de Vertebrados, Museo Nacional de Historia Natural, Santiago de Chile, Chile; UCR, University of California at Riversleigh, California, USA; FMNH, Field Museum of Natural History.

Other abbreviations: Ma, megannum, one million years in the radioisotopic time scale; SALMA, South American Land Mammal Age.

Dental nomenclature: L, length; W, width; i, lower incisor; I, upper incisor; c, lower canine; C, upper canine; p, lower premolar; P, upper premolar; m, lower molar; M, upper molar; StA, StB, StC, StD, and StE, stylar cusps A, B, C, D, and E respectively.

Dental homologies

Polydolopid remains usually consist of teeth, dentary and maxillary fragments, thus preventing knowlegde of the complete dentary formula, particularly the upper one. Flynn & Wyss (2004) described the most complete skull of a polydolopid, *Kramadolops mckennai*, from the Early Oligocene of Chile. Based on the broken skull with four broken alveoli on the anterior margin, *K. mckennai* had a hypertrophied, laterally compressed I1, possibly a second, small incisive, a small canine and a P1. The upper dental formula would then be: I2, C1, P3, M3. However, Goin *et al.* (2010) reinterpreted it as follows: I3, C1, P2, M3 (see also: Beck, 2017) (Fig. 3A).

Several dentaries with an almost complete horizontal ramus were recovered, and it can be observed that the anterior formula is not homogeneous. In *K. abanicoi* (Flynn & Wyss, 1999) it appears to be the most generalized, having a hypertrophied first incisor, a vestigial tooth on the dentary ridge and p2-m3 (Fig. 3B). The small tooth was interpreted as a p1 by Flynn & Wyss (1999). However, Goin *et al.* (2010) interpreted it as a small vestigial canine. This interpretation is followed here.

The presence of a small canine on some species of polydolopids is difficult to assert, because few mandibular fragments preserve the anterior region. In the specimen MACN-A 1334, here regarded as *Eudolops tetragonus*, two alveoli can be seen on the anterior margin of the tooth. One should be the hypertrophied first incisor, while the second, smaller one, could pertain to a small canine, perhaps larger than on *K. abanicoi*. Beck (2017) argued that three anterior teeth could be present on the specimen MACN-A 10340, a broken mandibular fragment with no teeth but with some partially preserved alveoli (here tentatively referred to *E. tetragonus*) (following Marshall, 1982). Because of the relative position and size, the large tooth could be the canine. However, he recognized that Ameghino (1903) had indicated the presence of two rather than three, alveoli, and because of the absence of teeth, the assignation of this specimen to any Polydolopid should be tentative. The latter is considered in this work. The generalized dental formula should then be i1,?c1, p1, m3, but an extreme simplification occurs in some species, as in *Kramadolops maximus*, where the lower dental formula is: i1, c0, p1, m3 (see: Marhall, 1982; Goin *et al.*, 2010).

Polydolopidae has distinct molariform features (Fig. 3; Supporting information Appendix S1; Figs S1–S12) that need further description. The premolar formula is reduced in polydolopids: P2 and P3 in the upper dentition and p3 in the lower one. They are all blade-like structures [plagiaulacoid type *sensu* Ameghino (1897)], and the lower p3 is larger than the upper ones. Sometimes, a second lower premolar, p2, is present, but constitutes a vestigial structure with almost no crown leaning on the anterior root of the p3. *Molars are all multicuspidate, having the lower ones two cusp rows:* one labial and the other one lingual. The m1 has, in addition, a huge, high, anterior and centrally placed protoconid, giving it the aspect of being triangularly shaped. The m2 is clearly quadrangular and mesiolingually has a large cusp, the metaconid, behind this; it has a variable number of cusps, generally two, one accessory cusp and the entoconid (e.g. *Pliodolops rothi*) or three, when two accessory cusps plus the entoconid are present (e.g. *Pliodolops serra*). Labially, it usually has four cusps (paraconid, protoconid, accessory cusp and hypoconid; Fig. 3E), even though sometimes a second accessory cusp could appear (e.g. *Antarctodolops mesetaense*). Finally, the m3 is more triangularly shaped, like the m1, but in this case is the posterior edge the one who is reduced with respect to the anterior one. Finally, the m3 is subtriangular in shape, with a reduced distal edge.

The upper molars vary more than the lower ones amongst the genera. The M1 is usually the greater one of the upper molar row. In generalized forms, it has two rows of cusps: one lingual, with three cusps (paraconule, protocone and metaconule) and sometimes with a few supernumerary cuspules; and the other one labial, with four or more cusps (the stylar ones) (Fig. 3D). In some species there might appear more supernumerary cuspules labial to the stylar row, forming a second row

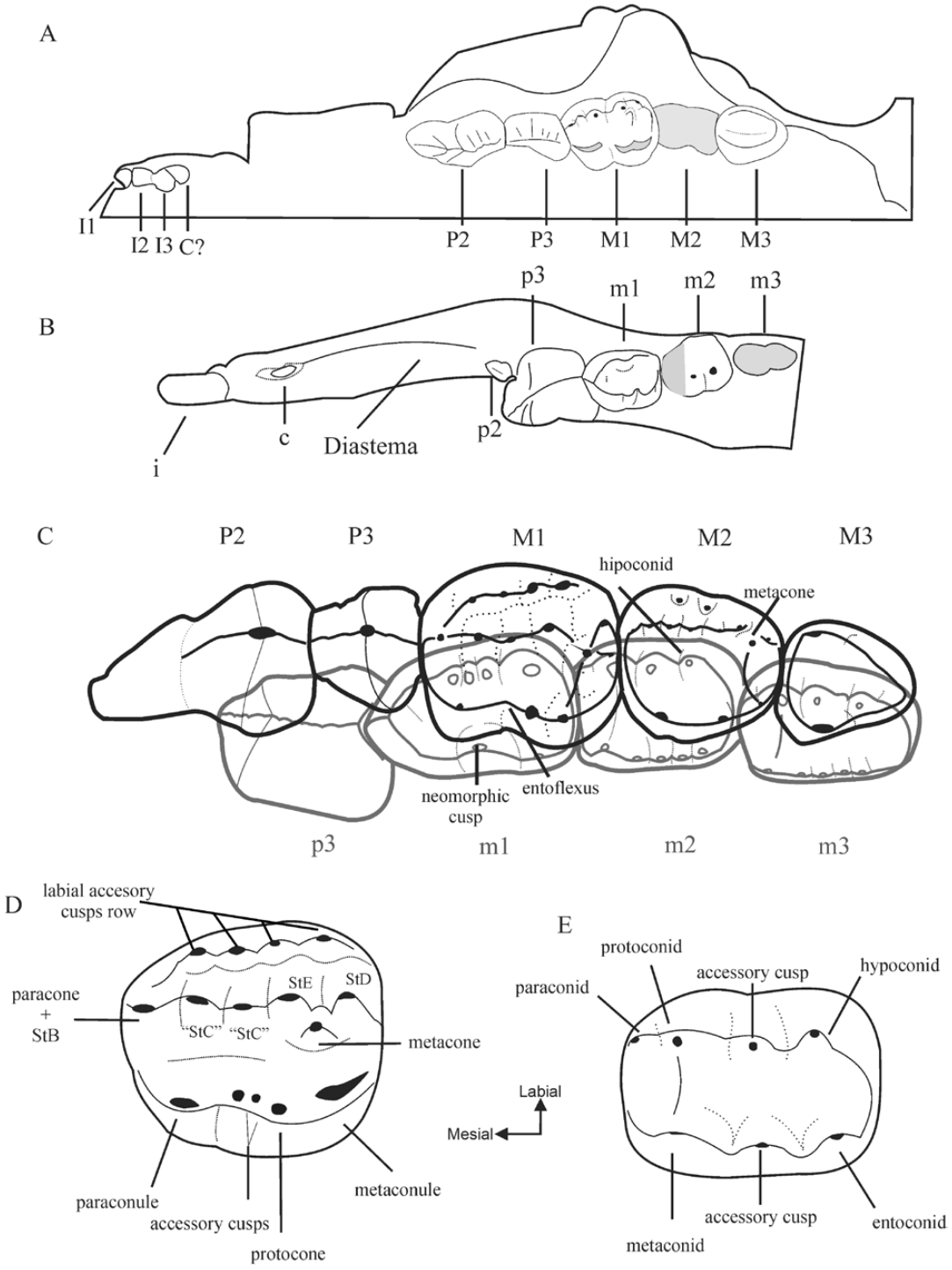

Figure 3. Schematic drawings of upper and lower dentition of Polydolopidae. A, partial skull from *Kramadolops mckennai*. B, left dentary fragment from *Kramadolops abanicoi*. C, occlusion scheme, upper teeth in black, lower teeth in dark gray (modified from Chornogubsky *et al.*, 2009). D, M1 outline drawing showing cusp homologies. E, m2 outline drawing showing cusp homologies.

(e.g. *Antarctodolops dailyi)*, or disorderedly placed (*Pliodolops rothi*). The M2 is usually much shorter than the M1 (except in *Eudolops* and *Kramadolops*) and has three lingual cusps and frequently one labial, stylar row. The M3, small in every polydolopid except for *Eudolops*, is triangularly shaped.

Polydolopids have, as described above, one of the most singular molar patterns seen in marsupials, and the homology of their cusps is, therefore, difficult to assert. In this work, the homologies of Chornogubsky *et al.* (2009) are followed, since they represent a synthesis and modification from previous hypotheses erected by Woodburne & Zinsmeister (1984) and Goin *et al.* (2003) (Fig. 3C–E).

RESULTS

PHYLOGENETIC ANALYSIS

After a cycle of tree bisection and reconnection (TBR) with 1000 replications and saving ten trees per replication, and a second cycle of TBR with the trees saved on the RAM, the algorithm found 243 equally parsimonious trees of 107 steps. The consistency (Ci = 0.598) and retention (Ri = 0.73) indices were calculated for all trees. Bremer support was equal to 1 on every internal node.

The topology of the consensus tree (Fig. 4) does not show resolution for the relationships among Bonapartheriiformes, *Roberthoffstetteria nationalgeographica* and Polydolopidae, since they form a trichotomy. Polydolopidae is recovered as a monophyletic group and its internal relationships are better resolved. The base shows also a trichotomy, formed by Gen. et sp. indet. 1, *Archaeodolops clavulus*, and a clade forming the rest of the species. *Eudolops tetragonus* is the sister-group of *Polydolops thomasi* + the remaining Polydolopidae. Finally, two clades can be observed: one constituted by *Kramadolops* and the other by *Hypodolops sapoensis* gen. & sp. nov. + *Antarctodolops* spp. + *Amphidolops* spp. + *Pliodolops* spp., forming a tetrachotomy.

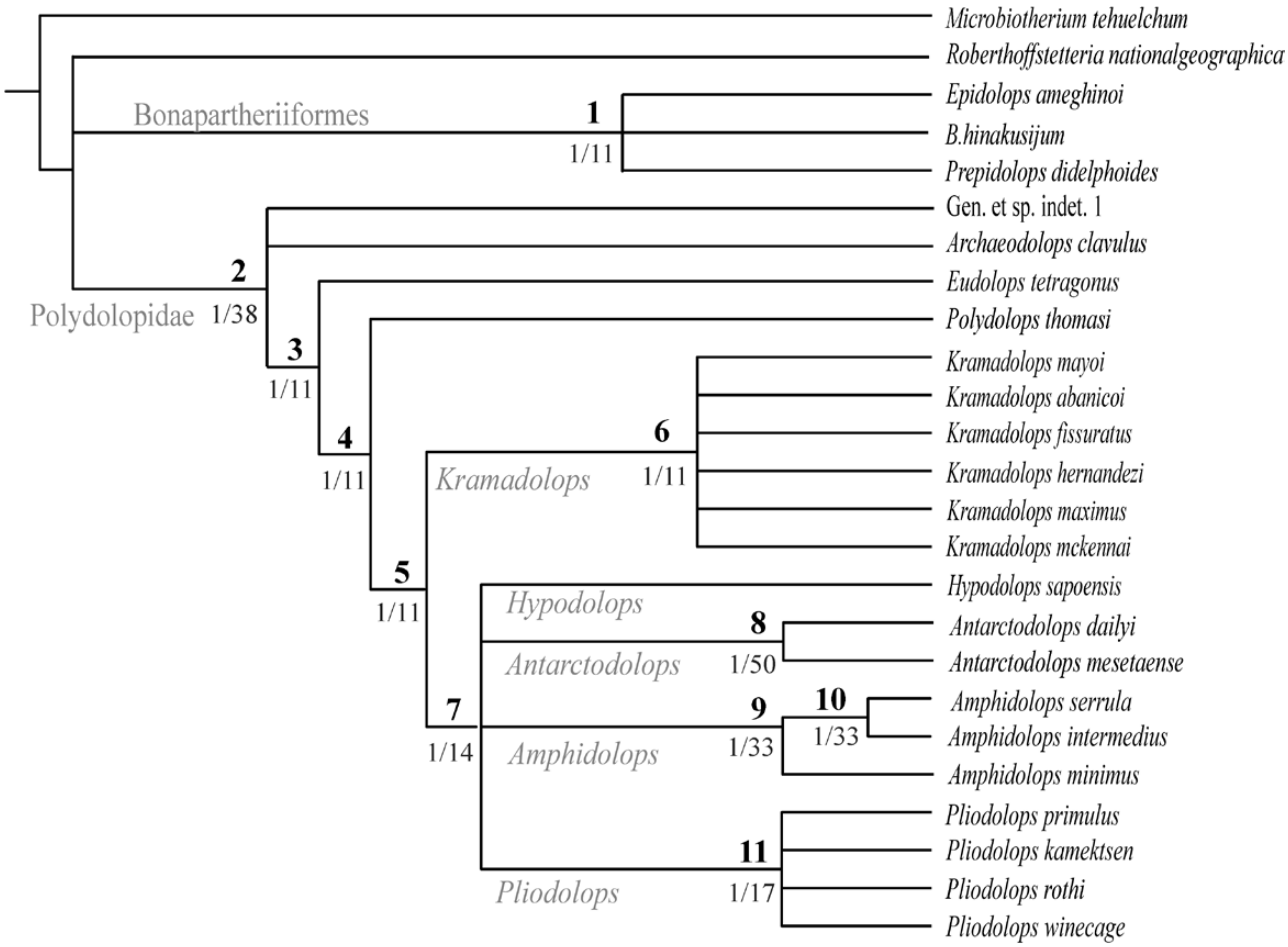

Figure 4. Consensus cladogram showing the relationships within Polydolopidae. In bold, above each branch, the node number. Below each branch, absolute/relative Bremmer support.

The synapomorphies (Supporting Information, Appendix S3) of *Kramadolops* include the presence of two labial ribs on the p3, a presence of ectoflexus on the M1, an M2 longer than wider, as well as the P3, and the presence of a labialized paraconid on the m2, but more lingually placed than the protoconid. The sister-group to *Kramadolops* is characterized by the presence of labial accessory cups on the M1 forming a row, and by having more than one cusp on the StC position.

The genus *Antarctodolops* has no p2, the length on the m1 is larger than on the p3, the enamel wrinkles are present and stark, even seen on worn molars, and there are two accessory cusps between the protoconid and the hypoconid on the m2. On the other hand, *Amphidolops* has no ectoflexus on the M1, more than one accessory cusp on the posterior lobe of the M1 and labial accessory cusps on the M1 forming a row, at the same level than the stylar row and partial or completely fused to it.

Finally, the genus *Pliodolops* is characterized by the absence of a large lingual cusp on the talonid of the m1, presence of lingual cusps on the m1 of different heights, the hypoconid on the m2 anteriorly projected, the paracone on M1 partially fused with the StB, and only one cusp on the StC position on the M1.

Systematic palaeontology

Infraclass Metatheria Huxley, 1880

Supercohort Marsupialia Illiger, 1811

Order Polydolopimorphia Marshall, 1987

Suborder Polydolopiformes Kinman, 1994

Family Polydolopidae Ameghino, 1897

Polydolopinae Pascual & Bond, 1981: 483

Type genus: *Polydolops* Ameghino, 1897.

Included genera: *Polydolops* Ameghino, 1897; *Eudolops* Ameghino, 1897; *Archaeodolops* Ameghino, 1903; *Kramadolops* Goin *et al.*, 2010; *Hypodolops* gen. nov.; *Pseudolops* Ameghino, 1902; *Antarctodolops* Woodburne & Zinsmeister, 1984; *Amphidolops* Ameghino, 1902; *Pliodolops* Ameghino, 1902.

Emended diagnosis: Marsupials with variable size, plagiaulacoid premolars and multicuspid molars. The generalized dentary formula is I /i 3/1, C/c 1/?1, P/p 2/2, M/m 3/3. They have an hypertrophied lower incisive, and probably the I1 as well, and a dorsal crest in the mandibular diastema; the mandible height at that area is markedly lower than the one having the molars; the trigonid on the m1 is conformed only by the protoconid; the m2 has one or two accessory cusps between the protoconid and the hypoconid; the m3 is triangular in occlusal view, with the posterior margin narrower than the anterior one; the molars usually present crenulated ('wrinkled') enamel; the upper molars have the para- and metaconule aligned with the protocone; the M1 has labially the StB-StE, being the first one partial or totally fused with the paracone and the StD to the metacone; the M1 also include labial accessory cuspules, that could be either isolated or forming a row; the M2 is usually shorter than the M1 and usually has only StB and StD among the stylar cusps; the M3 is small and triangular in shape in occlusal view.

Remarks: This family was first recognized by Ameghino (1897) to include the species here presented (and their synonyms). Later, Pascual & Bond (1981) included *Epidolops*, from the Palaeocene–Eoecene of Brazil, in this family (subfamily Epidolopinae). *Polydolops* and allies were included then in the subfamily Polydolopinae. Later, Goin *et al.* (2003) considered the family as only including polydolopines. This regard was later corroborated by Goin *et al.* (2009), who carried out a phylogenetic analysis where *R. nationalgeographica* was found as the sister-group of Polydolopidae, not *Epidolops* (see above). That is why from now on Polydolopidae is here regarded as a synonym of Polydolopinae.

Occurrence: Argentina (Patagonia), Chile (Central Chile) and the Antarctic Peninsula (Marambio/Seymour Island). Early Palaeocene–Early Oligocene.

Genus *Polydolops* Ameghino, 1897

Polydolops Ameghino, 1897: 497
Orthodolops Ameghino, 1903: 130
Anissodolops Ameghino, 1903: 148
Archaeodolops Ameghino, 1903: 150

Type species: *Polydolops thomasi* Ameghino, 1897.

Diagnosis: The same as for the species.

Occurrence: Patagonia, Argentina. Middle Eocene (Casamayoran and Mustersan SALMAs).

Polydolops thomasi Ameghino, 1897

(Fig. 5A, B, Appendix S4)
Polydolops *thomasi* Ameghino, 1897: 497; fig. 73
Polydolops simplex Ameghino, 1903: 185; fig. 119
Polydolops fur Ameghino, 1902: 39
Polydolops crassus Ameghino, 1902: 39
Orthodolops sciurinus Ameghino, 1903: 131; figs 54, 106
Pseudolops princeps Ameghino, 1902: 40 [in part]
Polydolops princeps Simpson, 1948: 62 [in part]

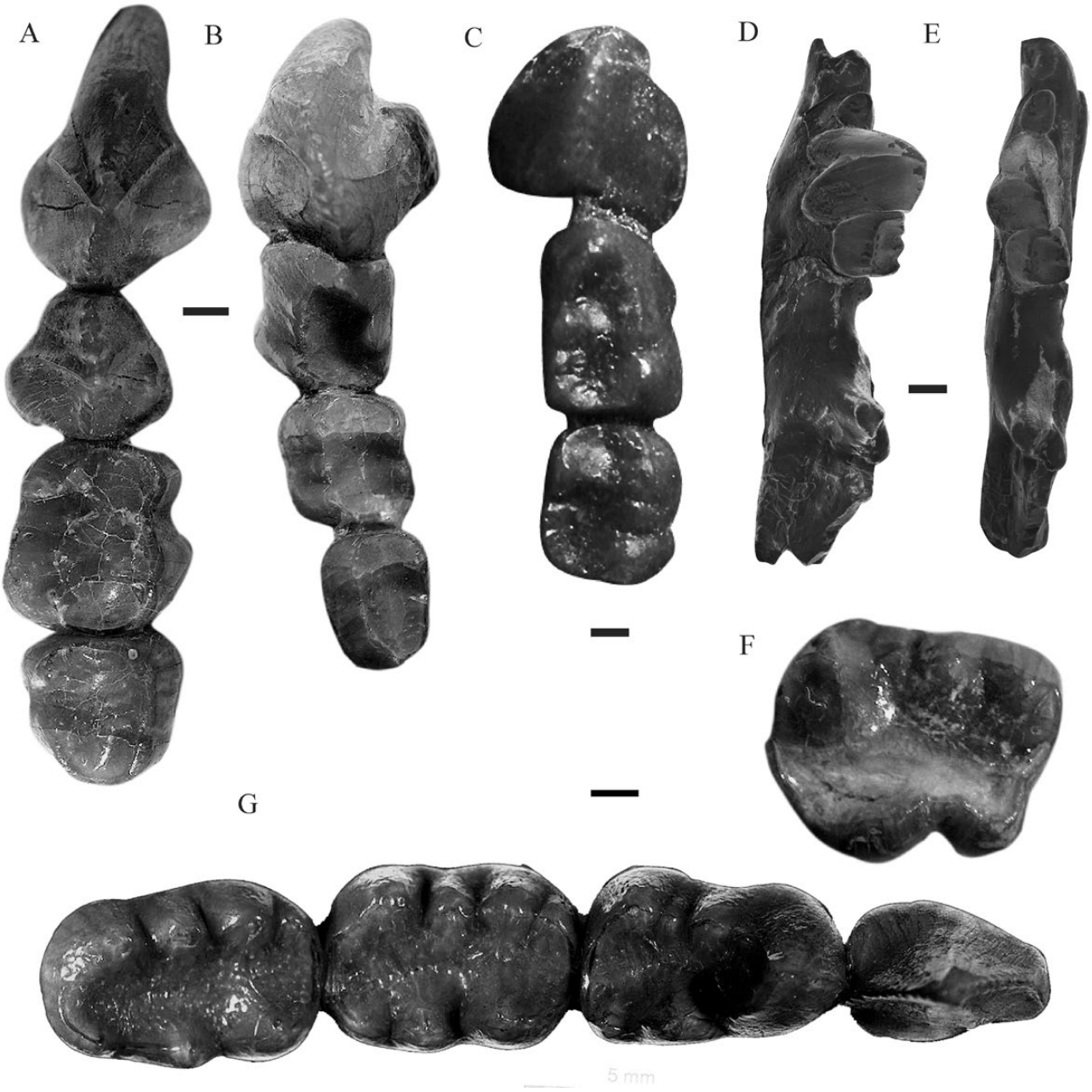

Figure 5. A, B, *Polydolops thomasi*. A, right P2-M2 from the lectotype (MACN-A 10338). B, left p3-m3 (MACN-A 10349). Both in occlusal view. C, *Polydolops* cf. *P. thomasi*. Occlusal view of right p3-m2 (MLP 52-XI-4–176). D, E, *Archaeodolops clavulus*. Left p2-m1 from the lectotype (MACN-A 10356). D, occlusolabial view. E, Occlusal view. F, G, *Eudolops tetragonus*. F, right M1 of the holotype (MACN-A 10358). G, left p3-m3 (MACN-A 10334). Both specimens in occlusal view. Scale bar = 1 mm.

Polydolops thomasi thomasi Simpson, 1948: 58; figs 1, 2, 8; pls 2, 4
Polydolops thomasi mara Simpson, 1948: 61; figs 3, 4; pl. 4
Polydolops thomasi paahi Simpson, 1948: 59; figs 1, 2; pl. 5
Polydolops thomasi crassus Simpson, 1948: 59; fig. 9; pl. 2

Lectotype: MACN-A 10338, a right maxillary fragment with P2-M2 (Fig. 5A).

Referred material: MACN-A 10335, a left dentary fragment with p3-m2 (holotype of *P. simplex*); MACN-A 10336, a fragment of right dentary with broken p2-m1, and complete m2-3 (holotype of *Orthodolops sciurinus*); MACN-A 10342, a right dentary fragment

with m1-3 (holotype of *P. fur*); MACN-A 10349, a left dentary fragment with p3-m3 (holotype of *P. crassus;* Fig. 5B); AMNH 28434, a right dentary fragment with p3-m2 (holotype of *P. thomasi paahi*); AMNH 28921, a fragment of left dentary with p3-m2 (holotype of *P. thomasi mara*); MACN-A 10332c, an isolated right m2; MACN-A 10332e, a right maxillary fragment with M1-2; MACN-A 10337, a right dentary fragment with p2-m3; MACN-A 10343, a right dentary fragment with m1-3; MACN-A 10350, a right dentary fragment with m1-2; MACN-A 10351, a left dentary fragment with p3-m2; MACN-A 10362a an isolated right M1; MACN-Pv 18469, a left dentary fragment with p2-3; MACN-Pv 18472, a left dentary fragment with m1-2; MACN-Pv 1261, an isolated right m2; MLP 59-II-28–81, a left dentary fragment with p3 and m2; MLP 59-II-28–83, a left dentary fragment with p3; MLP 59-II-28–84, a left dentary fragment with roots of p3-m1 and complete m2-3; MLP 59-II-28–85, a right dentary fragment with m1-2 and the roots of p3; MLP 59-II-24–716, an isolated left p3; MLP 59-II-24–38, an isolated right m2; MLP 59-II-24–659, an isolated right m1; MLP 66-V-4–21, a left dentary fragment with p3-m2; MLP 66-V-4–22, a right dentary fragment with m1-3; MLP 66-V-4–23, a left dentary fragment with p3-m1; MLP 66-V-4–24, a left maxillary fragment with M1-2; MLP 69-III-28-28, a left dentary fragment with m2-3; MLP 69-III-24-12, an isolated left p3; MLP 83-III-1–163, isolated right M2 and P3; MLP 83-III-1–164, an isolated left m1; MLP 87-XII-1-1, a left maxillary fragment with P2-M2; FMNH P14717, a left dentary fragment with m1-2; AMNH 28420, an isolated right M2; AMNH 28424, an isolated right M1; AMNH 28440, a left maxillary fragment with P3-M3; AMNH 28443, an isolated left p3; AMNH 28444, a right dentary fragment with p2-m1; AMNH 28449, a left isolated p3 and M2; AMNH 28920, an isolated right m2; AMNH 28924, an isolated right M1; AMNH 28925, an isolated right M1; AMNH 28926, an isolated right m2; AMNH 28927, an isolated right m1; AMNH 28930, a dentary fragment with p3; AMNH 28931, a left dentary fragment with m2; AMNH 28934, an isolated right p3.

Tentatively referred material: AMNH 28428, an isolated right m2; MLP 59-II-28–96, a right dentary fragment with p3-m2.

Emended diagnosis: Relatively large species of polydolopide, although smaller than *Eudolops* and *Kramadolops*. It has a proportionately large and strongly asymmetrical p3, with the posterior root considerably larger than the anterior one. It differs from other polydolopids, except for *Eudolops* spp. and *Kramadolops* spp., in having fewer accessory cusps on the molars. The m1 is similar in length to the m3 and has four lingual cusps (the second one large) and four to five labial cusps; the m2 has four labial cusps and three or four lingual; P2 is considerably wider and longer than P3, the latter being wider than long; on the M1 there are scatter labial cusps not forming a row. The paracone is not completely fused with the StB. The M2 is a lot smaller than the M1, but larger than the M3. The latter is small (similar in size to the one from *Amphidolops* spp. but smaller than the species of *Eudolops*).

Temporal and geographic distribution: All specimens were recovered from the Middle to Late Eocene of Patagonia, Argentina. In particular, specimens MACN-A 10336, MACN-A 10337, MACN-A 10338, MACN-A 10343, MACN-A 10350 and MACN-A 10351 were collected from beds of the 'Notostylopense' or '*Couches à Notostylops*' (Ameghino, 1902); MACN-A 10332c, MACN-A 10332e, MACN-A 10335, MACN-A 10342, MACN-A 10349, MACN-A 10362a, MACN-Pv 18469, MACN-Pv 18472, FMNH P14717, AMNH 28434, AMNH 28443, AMNH 28449 and AMNH 28934 were recovered from Gran Barranca; MACN-Pv 1261, AMNH 28420, AMNH 28424, AMNH 28428, AMNH 28440 and AMNH 28444 come from Cañadón Vaca; MLP 59-II-24–716 and MLP 59-II-24–659 come from Laguna de la Bombilla; MLP 87-XII-1-1 was recovered from the Southern cliffs of Valle Hermoso; MLP 59-II-28–81, MLP 59-II-28–83, MLP 59-II-28–84, MLP 59-II-28–85, MLP 59-II-24–38, MLP 66-V-4–21, MLP 66-V-4–22, MLP 66-V-4–23, MLP 66-V-4–24 and MLP 69-III-28-28 were recovered from Laguna de la Bombilla;. MLP 83-III-1–163 and MLP 83-III-1–164 were exhumed from the Southern slope at Valle Hermoso; AMNH 28920, AMNH 28921, AMNH 28924, AMNH 28925, AMNH 28926, AMNH 28927, AMNH 28930 and AMNH 28931 come from Rinconada de Los López; MLP 69-III-24-12 was recovered from La Gran Hondonada; MLP 59-II-28–96 comes from Cerro Conhué.

Measurements: Appendix S4

Remarks: This species was based on a maxillary fragment with P2-M2 and a fragment of isolated incisor (Ameghino, 1897). Both Simpson (1948) implicitly and Marshall (1982) explicitly, admitted that the incisor mentioned by Ameghino was not among the MACN collections. Simpson (1948) chose the maxillary fragment as type but it was Marshall (1982) who formally selected it as the lectotype.

Along with *Eudolops tetragonus*, *P. thomasi* was used in order to recognize the family Polydolopidae (Ameghino, 1897). In successive years, Ameghino (1902, 1903) assigned new material to it, including lower dentition, and also recognized new species for the genus: *P. simplex*, *P. crassus* and *P. fur*. For every one of these he assigned a single mandible with different

teeth preserved. These species were considered as junior synonyms of *P. thomasi* by Simpson (1948). Other species described by Ameghino (1902, e.g. *Orthodolops sciurinus* and *Pseudolops princeps*), were later also synonymized under *P. thomasi* by Marshall (1982).

With the species recognized by Ameghino (1897, 1902, 1903), Simpson (1948) acknowledged three groups in the genus *Polydolops*: (1) *Polydolops thomasi* group, (2) *Polydolops serra* group and (3) *Polydolops clavulus* group. The first one includes two subgroups: (a) *P. thomasi*, *P. fur* and *P. simplex*, all synonyms of *P. thomasi*; and (b) *Polydolops crassus* and *Orthodolops sciurinus*, being the latter synonym of the former. Simpson (1948) recognized four subspecies within *P. thomasi*: *P. t. thomasi*, *P. t. mara*, *P. t. paahi* and *P. t. crassus*. He argued that the small variation among them could be explained by geographic and/or temporal differences, because the specimens of the first one come from Cañadón Vaca, the second one from Rinconada de los López and the third and fourth from Gran Barranca. In his second group, Simpson (1948) included *Polydolops serra* and '*Anissodolops*' *serrifer*, both synonyms. The third group included a single species: '*Polydolops*' *clavulus*.

Marshall (1982) agreed with Simpson in that the species from the first group were synonyms of *P. thomasi*, but he did not distinguish them into subspecies. According to Marshall (1982), the conflict of using subspecies is that in extant populations they are allopatric, while some of Simpson's subspecies could have been living in sympatry. Moreover, he also assigned to *P. thomasi* part of the syntype from *Pseudolops princeps* (the maxillary fragment with M1-2 MACN-A 10332 e). He concluded that the differences in size of the jaws could be due to sexual, age, individual or geographical variation. However, even though there are some small differences among the specimens of the species, they should not be attributed exclusively to differences in procedence, because some of them come from the same site (e.g. MACN-A 10335, originally assigned to *P. simplex*; MACN-A 10343, *P. fur*, the latter larger and with more bulbous cusps; both from the Barrancan level from Gran Barranca).

The specimen MLP 69-III-24-12 (an isolated p3) was considered as '*Polydolops*' *mayoi* (Marshall, 1982). That species comes from the Mustersan levels at La Gran Hondonada (see below), but it is much smaller than the p3 from the holotype of *K. mayoi* and its features are more similar to the ones present in *P. thomasi.*

POLYDOLOPS CF. *THOMASI*

(FIG. 5C, APPENDIX S4)

Referred material: MLP 52-XI-4–176, a right dentary fragment with p3-m2.

Temporal and geographic distribution: The specimen comes from the Middle Eocene strata of Cerro Blanco, Chubut province, with no further data.

Measurements: Appendix S4.

Remarks: The material was assigned to '*Polydolops*' *mayoi* by Marshall (1982a). Marshall (1982) also argued that *P. thomasi* and '*P*'. *mayoi* are similar and considered their differences as mainly about proportions. Flynn & Wyss (1999) argued that the specimen MLP 52-XI-4–176 was possibly *Polydolops thomasi*. As can be established after the phylogenetic analysis, the species of *Kramadolops* have a few features that are as different as the ones presented in *P. thomasi.* One of them is the presence of two labial ribs on the p3 instead of one, as is common in polydolopids, as well as being larger than *P. thomasi*. Specimen MLP 52-XI-4–176, presents only one labial rib on the p3, which is also smaller than the one from *K. mayoi*. Overall morphology and size are more similar to the one of *P. thomasi*. However, as was observed by Marshall (1982), the molar proportions (as well as size) are different, because the m1 is proportionately longer and m2 shorter in this specimen than in *P. thomasi*, that is why it is here regarded as *Polydolops* cf. *P. thomasi*.

Marshall (1982) commented that MLP 52-XI-4–176 was collected by Roth from the 'T.i.C.B.' [= Terciario inferior de Cañadón (or Cerro) Blanco] (Marshall 1982: 44). This locality has been never relocalized, even though it apparently lies near Scarrit Pocket. The age of the levels where the specimen has been exhumed are uncertain, but some authors consider that they could be Mustersan–Tinguiririan in age (Flynn & Wyss, 2004).

GENUS *ARCHAEODOLOPS* AMEGHINO 1897

Polydolops Ameghino, 1902: 40 [in part]
Archaeodolops Ameghino, 1903: 150

Type species: Polydolops clavulus Ameghino, 1902.

Included species: Only the type species.

Diagnosis: The same as for the species.

Distribution: Patagonia, Argentina. Middle Eocene (*Ernestokokenia* fauna and Casamayoran SALMA).

ARCHAEODOLOPS CLAVULUS (AMEGHINO, 1902)

(Fig. 5D, E, Appendix S4)
Polydolops clavulus Ameghino, 1902: 40
Archaeodolops clavulus Ameghino, 1903: 150; figs 75, 103

Polydolops clavulus Simpson, 1948: 61
Polydolops clavulus Marshall, 1982*: 17; figs* 9–12

Lectotype: MACN-A 10356, a left dentary fragment with p2-m1 (Fig. 5D, E).

Paralectotype: MACN-A 10360, a right dentary fragment with p3-m2.

Referred material: MLP 79-I-17-3, an isolated left p3.

Emended diagnosis: Polydolopid with gracile mandible and small in size. The p3 is asymmetrical and has a simple molar structure, without enamel crenulations and with three sharp lingual cusps on the m1. It differs from most polydolopids, except for *Eudolops*, in having p3 with its roots included in the alveoli at the same level. It differs from other polydolopids, except from the species of *Kramadolops* and *Eudolops*, by having few accessory cusps in their molars. It differs from *Kramadolops*, except for *K. mayoi*, by possessing p2. It differs from *Kramadolops* and *Eudolops* by having asymmetrical p2 and molars with sharp and buccolingually compressed cusps. It is different from *Hypodolops* by lacking a posterolabial rim on the m1 and labial rims on the m2.

Temporal and geographic distribution: The specimens labelled MACN-A are of Casamayoran SALMA from Patagonia, Argentina, from the '*Couches à Notostylops*' *sensu* Ameghino (1902) with no additional data. MLP 79-I-17-3, came from Bajo de la Palangana, Chubut Province.

Measurements: Appendix S4.

Remarks: Ameghino (1902) originally recognized the species *Polydolops clavulus*, but he renamed it to include it in his new genus *Archaeodolops* (Ameghino, 1903). The main difference that he noted, to separate the species from the genus *Polydolops*, was the lack of serrations on the crests of the p3. Later, Marshall (1982) noted that the serrations were weak, probably due to wear. Even though Marshall's observations are accurate, the phylogenetic analysis reveals that *A. clavulus* is indeed a valid species and is not part of the genus *Polydolops*.

When Ameghino (1903) recognized the genus *Archaeodolops* he figured a mandible with p2-m2 and alveoli for the p1 and m3. There is no mandible in the MACN collections with these features. However, it is possible that Ameghino (1903) reconstructed the mandible using two different specimens: MACN-A 10356, a left dentary fragment with p2-m1, and MACN-A 10360, a right dentary fragment with p3-m2. Simpson (1948) chose MACN-A 10356 as the type. Later, Marshall (1982) suggested that both specimens could be part of the same individual (there is no definitive evidence to conclude about this statement) and formalized MACN-A 10356 as the lectotype.

About the reconstruction from Ameghino (1903), he figured a p1 in its mandible. However, this locus cannot be seen, as was previously observed by Simpson (1948) and implicitly accepted by Marshall (1982). It is possible that Ameghino interpreted as an alveolus a small discontinuity in one of the mandibles (MACN-A 10356), here interpreted as a problem of preservation and not an actual locus. When Flynn & Wyss (1999) described '*Polydolops*' *abanicoi* (*Kramadolops* in this work), they observed the presence of a little uniradiculated tooth behind the large procumbent anterior tooth. Following the interpretations of the anterior dentition presented by Marshall (1982a), they interpreted the small tooth as a canine (but see above). After that assumption, they accepted Ameghino's description of *A. clavulus* as having a small anterior tooth (dp1 for them; but not accepted here, see above).

Genus Eudolops Ameghino, 1897

Eudolops Ameghino, 1897: 94
Propolymastodon Ameghino, 1903: 100

Type species: Eudolops tetragonus Ameghino 1897.

Included species: The type species and *E. carolia-meghinoi* Marshall, 1982.

Emended diagnosis: The genus *Eudolops* is characterized by having large size, robust mandibles with molars with fewer accessory cusps when compared with other genera, but with well-defined large cusps; they lack p2 and have small p3. The latter is symmetrical in lateral view with acuminated apex.

Occurrence: Patagonia, Argentina. Middle Eocene (Casamayoran SALMA).

Eudolops tetragonus Ameghino, 1897

(Fig 5F, G)

Eudolops tetragonus Ameghino, 1897: 94; fig. 74
Propolymastodon caroli-ameghinoi (sic!) Ameghino, 1903: 100; figs 18, 22
Propolymastodon cardatus Ameghino, 1903*: 105; fig.* 23
Eudolops caroli-ameghinoi (sic!) Simpson, 1948: 67; fig. 10; pls 2, 7
Eudolops tetragonus Marshall, 1982a: 62, figs 50, 52, 56, 57 [in part]

Holotype: MACN-A 10358, an isolated right M1 (Fig. 5F).

Referred material: MACN-A 10334, a left dentary fragment with p3-m3 (holotype of *Propolymastodon caroliameghinoi*) (Fig. 5G); AMNH 28435, a right dentary fragment with m2-3; MLP 59-II-28–79, a right dentary fragment with a broken m2; MLP 59-II-28–80, a left dentary fragment with m2-3.

Tentatively referred material: MACN-A 10333, a left dentary fragment with m1-2 (holotype of *Propolymastodon cardatus*); MACN-A 10340, an edentulous dentary fragment; MLP 83-III-1–168, an isolated left m2; MLP 83-III-1–162, an isolated left m1; MLP 83-III-1–167, a right dentary fragment with p3.

Emended diagnosis: Larger species of the genus and with a more simplified molar structure. The M1 has only four labial cusps (StB-StE) and the metacone is fused with StE (it is distinguishable and between StD and StE on *E. caroliameghinoi*).

Temporal and geographic distribution: All specimens were recovered from Middle Eocene strata of Patagonia, Argentina. The holotype comes from the Casamayoran SALMA or '*Couches à Notostylops*' *sensu* Ameghino (1902) with no additional data. Materials MLP 59-II-28–79 and MLP 59-II-28–80 were collected from Laguna de la Bombilla locality; AMNH 28435 comes from Cerro Blanco; and MLP 83-III-1–168, MLP 83-III-1–162 and MLP 83-III-1–167 from the Southern slope of Valle Hermoso. Finally, MACN-A 10333, MACN-A 10334 and MACN-A 10340, as well as the holotype, were exhumed from levels of the *Couches à Notostylops* (Ameghino, 1902) with no further data.

Measurements: Appendix S4.

Remarks: Originally, the holotype (MACN-A 10358) was assigned to an M1 (Ameghino, 1897), but later Simpson (1948) considered it an M2. In this work, Ameghino's original appreciation is followed.

'*Propolymastodon*' *caroliameghinoi* was first described by Ameghino (1903) to include a dentary fragment with p3-m3. He also included *P. cardatus* in the genus, and related both species with *Promysops* acuminatus. In its original description of *Promysops acuminatus*, Ameghino (1902) included.

In its original description of *Promysops acuminatus*, Ameghino (1902) included a mandibular fragment with partial alveoli for two biarticulated teeth, the root of a hypertrophied incisor and alveoli for two uniradiculate teeth. Later, he assigned to the same species an isolated M3 (Ameghino, 1903). Both specimens had the same number in the collection (MACN-A 10340). Simpson (1948) only consider the mandibular fragment and synonimized *Promysops* with *Eudolops*. However, he preserved the identity of *E. acuminatus* and assigned to the species the holotype of *Propolymastodon cardatus* Ameghino, 1903, a mandibular fragment with m1-2 (MACN-A 10333). Marshall (1982) regarded Simpson's view as correct, and he also synonymized *E. caroliameghinoi* (Ameghino, 1902) with *E. tetragonus*, describing and photographing not only the type of *P. acuminatus*, but also the isolated M3 described by Ameghino (1903). The M3 is currently lost from the MACN collection, which is why it was not included in this review. However, based on the figure presented by Ameghino (1903), it may have been referred to *E. caroliameghinoi*.

Simpson (1948) referred a maxillary fragment with M1-3 (AMNH 28932) to *E. tetragonus*. However, Marshall (1982a) recognized a new species from this material: *E. hernandezi* (= *Kramadolops hernandezi*). In the present work, *E. tetragonus* is considered as represented by the specimen from the holotype, and the lower mandibles and teeth mentioned above.

Promysops acuminatus is not regarded as a polydolopid, because the mandibular fragment suggests more antemolar teeth that the amount present in Polydolopidae. Moreover, it does not show the mental foramina common to Polydolopidae: one ventral to the p3-m1 boundary and the other ventral and mesial to p2.

The specimens MLP 77-VI-14–5, a right maxillary fragment with P2-M2 (Fig. 10A), and AMNH 28437, an isolated left M3, were previously assigned to the species by Marshall (1982), but are here assigned to Gen et sp. indet. 1, since the molars have stark differences with the holotype, having an M1 with more and proportionally smaller cusps, and the metacone only partially fused with the base of StE (completely fused and hypertrofied in *E. tetragonus*). The stylar cusps StB and StC are not aligned (i.e. StB is more lingually placed than StC) and present a well-developed ectoflexus (this is not seen in the holotype or in the lower teeth).

EUDOLOPS CF. *TETRAGONUS*

Referred material: MLP 83-III-1–167, an isolated left p3.

Temporal and geographic distribution: The specimen comes from the Middle Eocene strata outcropping on the Southern Cliff of Valle Hermoso, Chubut Province.

Measurements: Appendix S4.

Remarks: The specimen is similar to the p3 of *Eudolops tetragonus*, but it has two differences: (1) the posterior border is higher than the anterior one, thus being asymmetrical in lateral view, as occurs in *E. tetragonus*; (2) the specimen is proportionately wider posteriorly than in *E. tetragonus*.

Genus *Kramadolops* Goin *et al.*, 2010

Polydolops Odreman Rivas, 1978 [in part]
Eudolops Marshall 1982*a* [in part]

Type species: Polydolops mayoi Odreman Rivas, 1978.

Included species: The type species and *K. abanicoi* (Flynn & Wyss, 1999); *K. mckennai* (Flynn & Wyss, 2004); *K. fissuratus* Goin *et al.*, 2010; *K. maximus* Goin *et al.*, 2010; *K. hernandezi* (Marshall, 1982).

Emended diagnosis: It differs from other genera, except for *Polydolops* and *Eudolops*, by having an m2 with vestigial paraconid, more lingually placed than the protoconid, in the anterior margin of the tooth. It differs from other genera by having bulbous upper and lower molars with few cusps, and upper molars with no labial accessory cusps and subdivided in two lobes, anterior and posterior. Differs from *Eudolops* by having upper premolars of different sizes, the anterior one being larger (but narrower) than the posterior. The p3 is asymmetrical in lateral view and its posterior crest is longer and more subhorizontal than the anterior one, as in *Polydolops*, but is strongly compressed laterally. The p3 has two labial ribs (and in some cases also two lingual ribs as well).

Remarks: Representatives of this genus have the latest records of known polydolopids. The only known skull corresponds to the one of *K. mckennai*, from the Tinguiririan of Chile (Flynn & Wyss 2004). The largest polydolopid is also from this genus: *K. maximus* (Goin *et al.* 2010). The dentary formula for this genus is: I3/i1, C1/c1, P2/p2, M3/m3 (but see above). The formula is extremely reduced in *K. maximus*, where both the canine and the p2 disappear (convergently with *Eudolops*).

Distribution: Argentina (Chubut Province) and Central Chile. Late Eocene to Early Oligocene (Musteran and Tinguiririan SALMAs).

Kramadolops mayoi (Odreman Rivas, 1978)

(Fig. 6A, B, Appendix S4)
Polydolops mayoi Pascual & Odreman Rivas, 1971: 381 *(nomen nudum)*
Polydolops mayoi Odreman Rivas, 1978*:* figs 36–38
Kramadolops mayoi Goin *et al.*, 2010

Holotype: MLP 69-III-24-1, a right dentary fragment with part of the incisor and p3-m2 (Fig. 6A, B).

Referred material: MLP 59-II-28–135, a left dentary fragment with m1-2 and the roots of m3.

Tentatively referred material: MLP 59-II-28–95, a left dentary fragment with m1-2 and roots of p3.

Emended diagnosis: This is the smallest species of the genus and the one with wider p3. It differs from the species with known p3 by having incomplete labial ribs. It differs from *K. maximus* by having p2 and m2 larger than m1. It differs from *K. fissuratus* by having a larger labial accessory cusp on the m2, well separated from the protoconid.

Temporal and geographic distribution: All specimens come from Late Eocene levels from Chubut Province. The holotype was recorded from La Gran Hondonada; MLP 59-II-28–135 and MLP 59-II-28–95 were exhumed from Cerro Conhué.

Measurements: Appendix S4.

Remarks: The holotype has part of a large procumbent tooth, considered a canine by Marshall (1982) but most probably an incisor (see above). The specimen MLP 59-II-28–96, assigned to '*Polydolops*' *mayoi* by Marshall (1982), is here referred to *Polydolops thomasi* (see remarks under that species). The specimen MLP 59-II-28–135 is referred to *K. mayoi*, as was previously done by Marshall (1982). However, specimen MLP 59-II-28–95, also considered as *K. mayoi* by Marshall (1982), is here referred with doubts, due to the presence of a proportionately small m2 and absence of p2 (reduced but still present in the holotype).

Kramadolops abanicoi (Flynn & Wyss, 1999)

(Fig. 6C, D, *Appendix S4*)
Polydolops abanicoi Flynn & Wyss, 1999: 535; fig. 1
Kramadolops abanicoi Goin *et al.*, 2010

Holotype: SGOPV 2941, a left dentary fragment with part of the incisor, c1-m2, and roots of the m3 (Fig. 6C, D).

Emended diagnosis: Slightly smaller than *K. mckennai*, but larger than *K. mayoi*. It differs from *K. mayoi* by having a more gracile mandible, the m2 is proportionately shorter and molars in general are

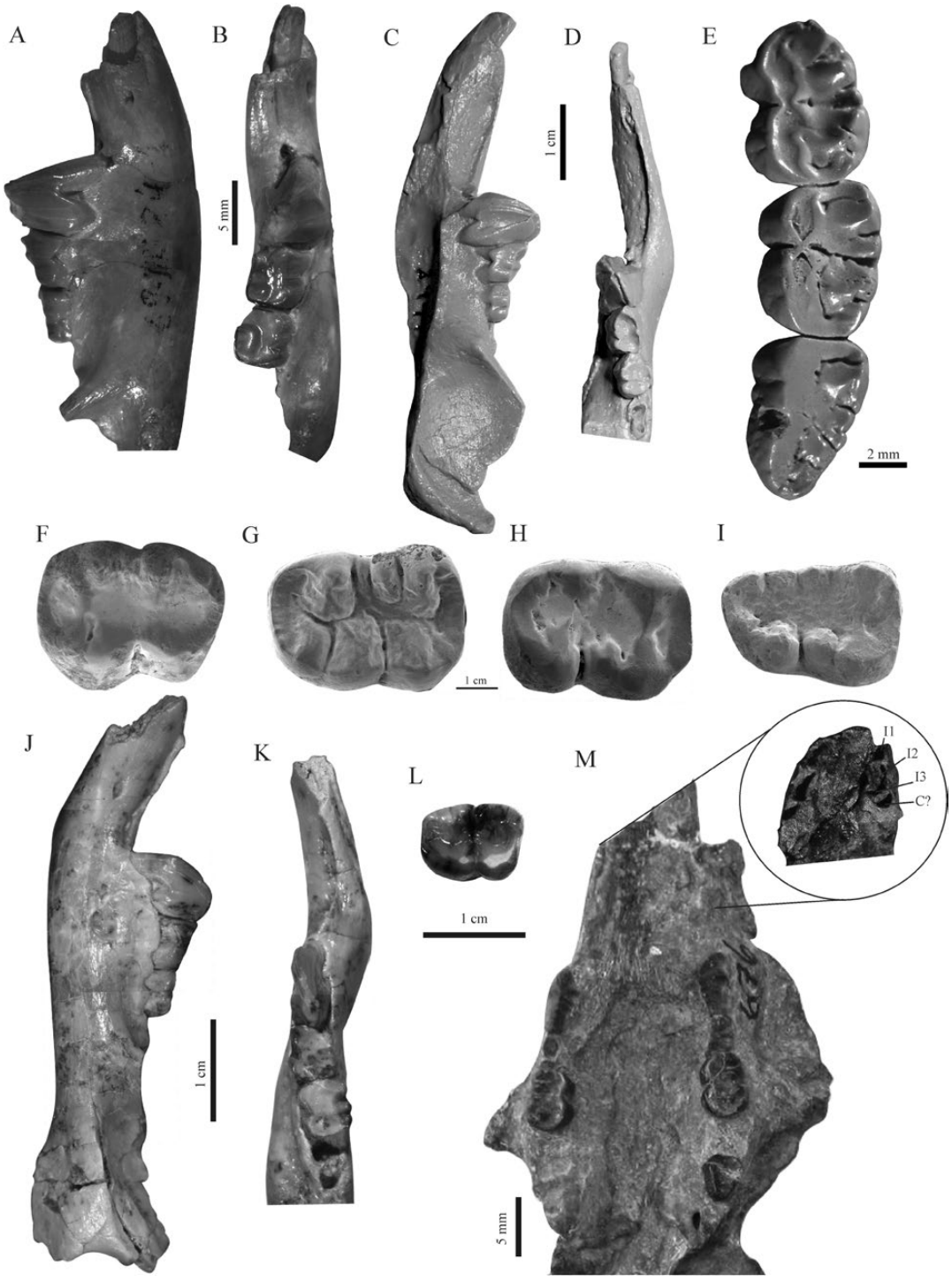

Figure 6. A, B, *Kramadolops mayoi*. Right mandible with broken incisive and p3-m2 from the holotype (MLP 69-III-24-1). A, labial view. B, occlusal view. C, D, *Kramadolops abanicoi*. Left mandible with broken incisive, p1, and p2-m2 from the holotype (SGOPV 2941, cast). C, labial view. D, occlusal view. E, *Kramadolops hernandezi*. Left mandible with M1-3 from the holotype (AMNH 28932). Occlusal view. F–I, *Kramadolops fissuratus*. F, left M2 (MPEF-PV 4343). G, right M1 from the holotype (MPEF-PV 4342, mirror image). H, right m2 (MPEF-PV 4339). I, right m3 (MPEF-PV 4340). All specimens in occlusal view. J–L, *Kramadolops maximus*. J, K, left mandible with p3-m2 from the holotype (MPEF-PV 4500). J, occlusal view. K, labial view. L, Left M1 (MPEF-PV 4501) in occlusal view. M, *Kramadolops mckennai*. Skull fragment with right P2 and M1, and left P2-M1, and M3 from the holotype (SGOPV 3476) in palatal view with detail of the snout on palatal view.

less robust. It differs from *K. maximus* by having p2, a wider p3 and m1 proportionately smaller (shorter than the p3). In addition, molars do not have the labial accessory cusp so lingually placed when compare with the protoconid and hypoconid, as occurs in *K. maximus*. It is distinguished from *K. fissuratus* by having a m2 with a much less developed metaconid and cusps less differentiated. The m2 does not present two lobes so distinctly, as in *K. fissuratus*.

Temporal and geographic distribution: The specimen was recovered from the Early Oligocene of locality C-89-39, Termas del Flaco, Central Chile.

Measurements: Appendix S4.

Remarks: This species was originally assigned to *Polydolops* because of the presence of p2 and the overall morphology of the p3. However, Flynn & Wyss (1999) recognized that it possessed prominent labial ribs that, according to them, was similar to the type of the ones present in *Polydolops*. As previously stated, in this work, the presence of two labial carenae on the p3 is considered as a synapomorphy of *Kramadolops*. The presence of two labial ribs is only seen in *K. maximus*, but not in *K. mayoi*. Flynn & Wyss (1999) distinguished *K. abanicoi* from *Amphidolops* by the size of the cusps, considerably larger in *K. abanicoi*, and by the absence of enamel wrinkles. However, these wrinkles are common in several polydolopids and usually disappear after wear.

KRAMADOLOPS FISSURATUS GOIN *ET AL.*, 2010

(Fig. 6F–I, Appendix S4)

Holotype: MPEF-PV 4342, an isolated right M1 (Fig. 6G).

Referred material: MPEF-PV 4249, an isolated left P3; MPEF-PV 4327, an isolated right P3; MPEF-PV 4343, an isolated left M2 (Fig. 6F); MPEF-PV 4246, an isolated right P2; MPEF-PV 4298, an isolated right P2; MPEF-PV 4301, an isolated and broken right P3; MPEF-PV 4302, an isolated and broken P2; MPEF-PV 4317, an isolated and broken M1; MPEF-PV 4166, an isolated p3; MPEF-PV 4267, an isolated p3; MPEF-PV 4329, an isolated right m2; MPEF-PV 4338, an isolated right m2; MPEF-PV 4339, an isolated right m2 (Fig. 6H); MPEF-PV 4341, an isolated left m2; MPEF-PV 4328, an isolated left m2; MPEF-PV 4335, an isolated left m2; MPEF-PV 4315, an isolated right m3; MPEF-PV 4336, an isolated right m3; MPEF-PV 4340, an isolated right m3 (Fig. 6I); MPEF-PV 4303, an isolated and broken right m1.

Diagnosis (see Goin et al., 2010: 87): Differs from other species of the genus by having molars with deeper flexae and flexids (i.e. the anterior and posterior lobes are well differentiated). Differs from *K. mckennai*, *K. hernandezi* and *K. maximus* in having a posterior lobe larger than the anterior one on the M1 and by having a small cusp lingual to the ectoflexus. Differs from *K. mckennai* by having posterolabial cusps on M1 located more closely together. The p3 is more laterally compressed than in *K. mayoi* and *K. abanicoi*, but wider than that of *K. maximus*. Differs from *K. abanicoi* by having a more asymmetrical p3 in lateral view.

Temporal and geographic distribution: All specimens come from Early Oligocene levels from La Cancha, Chubut Province.

Measurements: Appendix S4.

Remarks: This species is the one that has cusps more difficult to homologize in the genus. It also possesses extremely reduced basins, especially on its upper molars, which are similar to the lower ones because of its well-defined and bulbous cusps.

KRAMADOLOPS HERNANDEZI (MARSHALL, 1982) **COMB. NOV.**

(Fig. 6E, Appendix S4)

Eudolops hernandezi Marshall, 1982: 70; figs 60, 61.

Eudolops tetragonus Marshall, 1982: 62 [in part]

Holotype: AMNH 28932, a left maxillary fragment with M1-3 (Fig. 6E).

Referred material: AMNH 28430, an isolated right M1.

Emended diagnosis: It differs from the other species of the genus by having subequal sized upper and proportionately longer molars, and by having two cusps in the position of StC on the M1.

Temporal and geographic distribution: Both specimens come from the Middle Eocene levels of Chubut Province. The holotype was exhumed from Rinconada de Los López and AMNH 28430 comes from Bahía Solano.

Measurements: Appendix S4.

Remarks: The specimens here described were originally assigned to *E. tetragonus* by Simpson (1948). Later, Marshall (1982) considered the maxillary fragment AMNH 28932 different enough to recognized

a new species: '*Eudolops*' *hernandezi*. The M1 AMNH 28430 was considered to be *E. tetragonus* by Marshall (1982). Here both specimens are considered as being part of the species (see above under *E. tetragonus* remarks) and after the phylogenetic analysis, also considered as part of *Kramadolops*.

Kramadolops maximus Goin *et al.*, 2010

(Fig. 6J–L, Appendix S4)

Holotype: MPEF-PV 4500, a left dentary fragment with p3-m2 (Fig. 6J, K).

Referred material: MPEF-PV 4501, an isolated left M1 (Fig. 6L).

Emended diagnosis: This is the largest species of the genus and differs from the other species by having a deeper exctoflexus and fused posterolabial cusps on the M1; it does not have p2 and the p3 is large, long and laterally compressed, with two labial and two lingual ribs; the dentary is longer and slender than the one of the other species of the genus.

Temporal and geographic distribution: Both specimens were recovered from the Early Oligocene levels of La Cantera locality at the Chubut Province.

Measurements: Appendix S4.

Remarks: Besides being the largest species of the genus, it is the one that presents the most reduced dentary formula, showing no p2 or canine. It also has a serrated and extremely compressed p3.

Kramadolops mckennai (Flynn & Wyss, 2004)

(Fig. 6M, Appendix S4)
Polydolops mckennai Flynn & Wyss, 2004*:* figs 6.1, 3.2
Kramadolops mckennai Goin *et al.*, 2010

Holotype: SGOPV 3476, a skull fragment with right P2 and M1, and left P2-M1, and M3 (Fig. 6M).

Emended diagnosis: Species larger than *K. mayoi* but smaller than *K. maximus*. Differs from the other species of the genus where the P2 is known by its buccolingual development, almost as important as in the P3. Differs from *K. fissuratus* by possessing the distal lobe of the M1 only slightly larger than the anterior one and by having the posterolabial cusps on the M1 nearer from each other.

Temporal and geographic distribution: The specimen was recovered from the Early Oligocene levels at Cachapoal locality, Central Chile.

Measurements: Appendix S4.

Remarks: The holotype and only known specimen of this species is a deformed and broken skull. However, the anterior broken margin of the skull can be seen and it includes a first, probably with some hypertrophy, I1, and then three more posterior alveoli, hypothesized here as I2, I3, and probably the canine, coincident with Goin *et al.* (2010; see above)

Originally this species was assigned to the genus *Polydolops* (Flynn & Wyss, 2004), mainly because of the development of the premolars and the small size of the M3. However, the authors recognized similarities in the molars with the ones present in the species of *Eudolops*. This combination of features encouraged Goin *et al.* (2010) to recognize the genus *Kramadolops*, an assignment that was supported by the phylogenetic analysis.

Genus ***Hypodolops* gen. nov.**

Polydolops Tejedor *et al.*, 2009 [in part]

Zoobank registration: urn:lsid:zoobank.org:act:9F2C6D4C-D2CB-49E3-BECD-54C3E050BCA0

Type species: Hypodolops sapoensis.

Included species: Only the type species.

Etymology: From Greek prefix υϖό, *hypo-*, under, referring to the small cusp situated under the labial talonid cusps on the m1 of the specimens from this genus. The suffix *-dolops* is commonly employed in genera of Polydolopidae and is likely derived from Greek δόλοϖες, deceit. The gender is masculine.

Diagnosis: The same as for the species.

Distribution: Chubut Province, Argentina. Middle Eocene (Paso del Sapo fauna).

Hypodolops sapoensis sp. nov.

(Fig. 7A–F, Appendix S4)
***Polydolops* sp. nov. 1** Tejedor *et al.*, 2009
***Polydolops* sp. nov. 2** Tejedor *et al.*, 2009

Zoobank registration: urn:lsid:zoobank.org:act:3A48B2BD-8D36-4453-84F3-E047559E28FB

Holotype: LIEB-PV 1153, a right maxillary fragment with M1-2. (Fig. 7A, B).

Referred material: LIEB-PV 1154, an isolated right m1 (Fig. 7D); LIEB-PV 1155, an isolated left m2

(Fig. 7E); LIEB-PV 1156, an isolated left m3; LIEB-PV 1157, an isolated left m2; LIEB-PV 1173, a right maxillary fragment with M1-2 (Fig. 7C); LIEB-PV 1158, an isolated right M1; LIEB-PV 1174, an isolated left M1; LIEB-PV 1175, an isolated right M1; LIEB-PV 1176, an isolated right M1; LIEB-PV 1177 an isolated right M1; LIEB-PV 1159, a right dentary fragment with p3-m1; LIEB-PV 1160, a left dentary fragment with broken m1-2; LIEB-PV 1163, an isolated left m1; LIEB-PV 1164, an isolated left m1; LIEB-PV 1165, an isolated right m1; LIEB-PV 1166, an isolated right m1; LIEB-PV 1167, an isolated right m1; LIEB-PV 1168, an isolated left m2; LIEB-PV 1169, a left dentary fragment with m2-3 (Fig. 7F).

Etymology: The epithet was chosen because specimens were found in the vicinity of Paso del Sapo (Chubut Province, Argentina).

Temporal and geographic distribution: All specimens come from Middle Eocene levels in the vicinity of Paso del Sapo, Chubut Province. The holotype, LIEB-PV 1154, LIEB-PV 1158, LIEB-PV 1160 and LIEB-PV 1163 were exhumed from levels of the Tufolitas Laguna del Hunco Formation at Laguna Fría. The other specimens come from levels of the Andesitas Huancache Formation at La Barda locality. Early to Middle Eocene.

Diagnosis: Small species of Polydolopidae characterized by having a proliferation of cusps in their molars. It differs from *Polydolops* spp. by having two rows of labial cusps on the M1 and two cusps in StC position. It differs from of *Antarctodolops* spp. and *Amphidolops* spp. by possessing distinguishable labial cusp rows on the M1 and not partially fused at the base, and by having a p3 longer than the m1. It differs from *Eudolops* by having molars with more accessory cusps and premolars proportionately much wider and asymmetrical in lateral view. It differs from *Kramadolops* spp. by having more accessory cusps in the molars and by having wider premolars (compressed in the species of *Kramadolops*). It differs from *Pliodolops* by possessing two cusps in the StC position on the M1 and by having the hypoconid more posteriorly placed. It differs from all other polydolopids by having a light ridge with a cuspule on it, at the labial wall of the m1.

Description: The holotype corresponds to a small, right maxillary fragment with the proximal part of the slender zygomatic arch, that runs dorsal to the distal half of the M1 and the mesial half of the M2. The M1-2 are well preserved, and are almost unworn; they show some wrinkles on the trigon basin, as well as on their lingual wall (these are more visible in LIEB-PV 1173 and LIEB-PV 1175). However, only part of the posterior root alveolus of the P3 and the mesiolabial and mesiolingual alveolus of the M3 are preserved from the other loci. The P3 was probably not large, and the M3 could have been almost as wide as the M2.

The M1 is larger than the M2 and has three cusp rows. Lingually, it has two main lobes: the mesial lobe is formed by the paraconule and mesial to it, a small cuspule is placed. The latter is not always evident, especially in worn molars (e.g. LIEB-PV 1173), but is usually present (e.g. LIEB-PV 1177). The posterior lobe has the protocone and, distal to it, separated by a light furrow, is the metaconule. Distal to the metaconule is a small cuspule. This cuspule cannot be seen on the specimen LIEB-PV 1173, but this could be due to wear, present in that region. Labially, the M1 shows two almost parallel cups rows, united mesially by a larger cusp (StB + paracone). The internal row has four cusps after the latter, two cusps at the StC position, a StD and the StE. These last two cusps are connected and basally fused to the metacone. The most labially placed row has five cusps, which are smaller than the stylar ones. The last cusp, more distally placed, is also the smallest.

The M2 is almost a third shorter and narrower than the M1 on the holotype. The only other M2 known for the species corresponds to the one present on LIEB-PV 1173 and is a little different in proportions, since it presents a labiolingual extension, larger than on the holotype. However, in both cases they have only two cusp rows: the lingual one formed by the aligned paraconule, protocone, and metaconule. The labial border of the tooth shows a StB, StC, and StD of similar sizes, and a small StE. The metacone is similar in height than the StD and is almost completely fused to it. At the labial wall, and between the StC and StD, lies a small supernumerary cuspule. This cuspule is better developed on LIEB-PV 1173.

Several lower molars and dentary fragments are assigned to this species based on size and cups development. Even though no complete jugal series was found for *H. sapoensis*, three dentary fragments are assigned to it: LIEB-PV 1159, with broken p3 and complete m1; LIEB-PV 1169, with complete m2-3; and LIEB-PV 1160, with broken m1-2. These specimens, plus several isolated molars, allow to understand the variation on the molar proportions and sizes, which includes a longer and larger m1, and a decreased on molar size from the m1 to the m3. On the other hand, the p3, only known on LIEB-PV 1159, is narrow and of moderate size, only a little longer than the m2, and with subequal long roots.

The m1, the larger molar of the row, has on its lingual side three large and buccolingually compressed cusps. The mesial one is on the distal end of the crest that descends from the trigonid cusp (the protoconid).

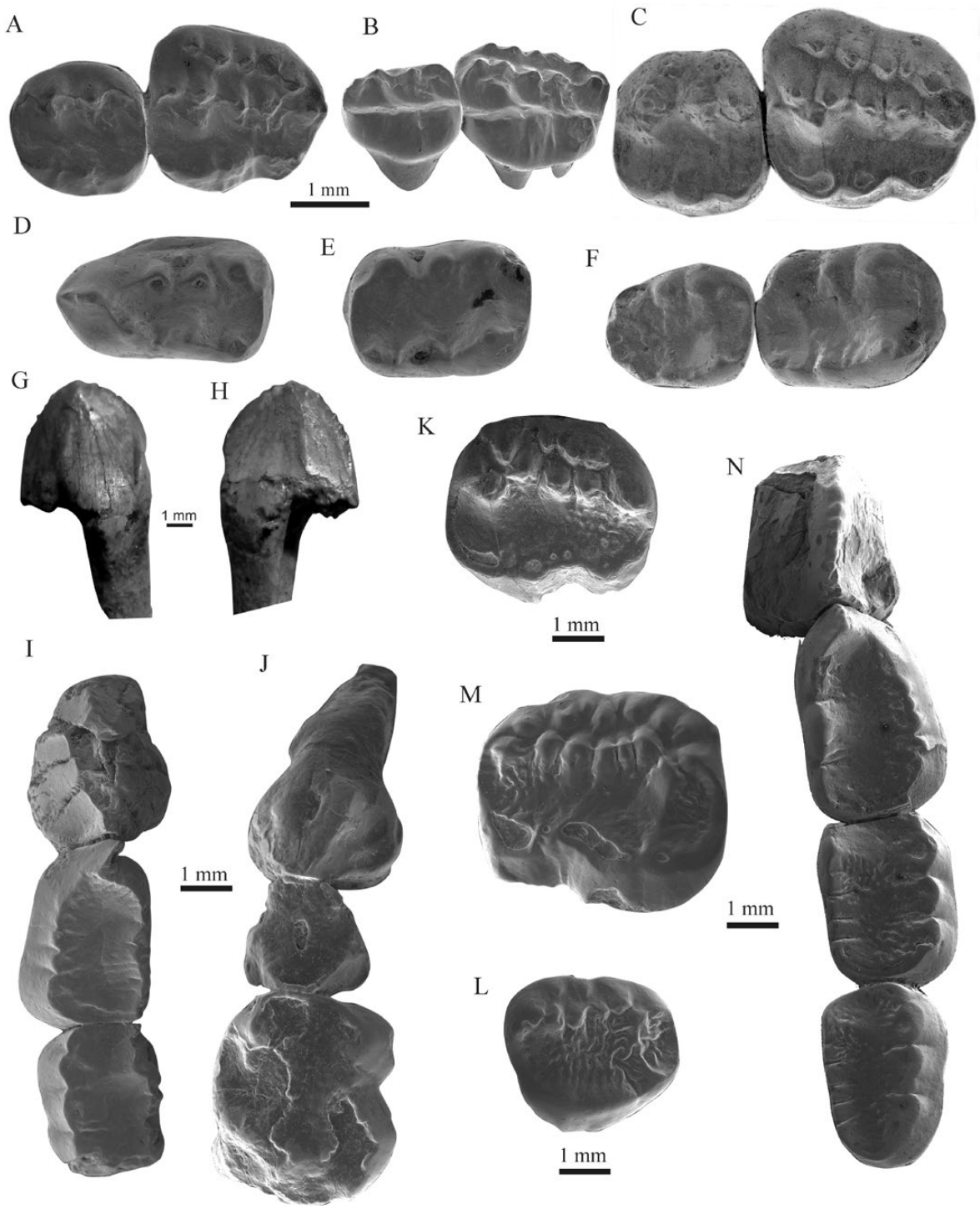

Figure 7. A–F, *Hypodolops sapoensis*. A, B, right M1-2 from the holotype (LIEB-Pv 1153). A, occlusal view. B, occlusolingual view. C, right M1-2 (LIEB-Pv 1173). D, right m1 (LIEB-Pv 1154). E, left m2 (LIEB-Pv 1155). F, left m2-3 (LIEB-Pv 1169). Except for B (in occlusolingual view), all specimens are in occlusal view. G, H, *Pseudolops princeps*. Left p3 from the lectotype (MACN-A 10332a). G, labial view. H, lingual view. I–K, *Antarctodolops dailyi*. I, left p3-m2 from the holotype (UCR 20910, cast). J, right P2-M1 (MLP 87-II-1-1). K, right M1 (MLP 88-I-1–4). All specimens in occlusal view. L, *Antarctodolops* sp. Left M2 (UCR 20913) in occlusal view. M, N, *Antarctodolops mesetaense.* M, left M1 (MLP 95-I-10–4). N, right p3-m3 from the holotype (MLP 96-I-5–12). All specimens in occlusal view.

Posterior to this cusp, occurs the largest cusp of the talonid, and distal to it, the entoconid, is the smallest of the lingual row. In some unworn specimens, as in LIEB-PV 1159, a small, fourth cuspule can be seen distal to the entoconid. On the labial margin, three (LIEB-PV 1154) or four (LIEB-PV 1159) cusps can be seen. The distal one, more labially salient, is the hypoconid, and mesial to it, the smaller and subequal supernumerary cusps (two or three). Below the latter, a small cuspule, usually on a slender ridge, lies on the labial wall of the m1.

The m2 is quadrangular in occlusal view and has three main cusps lingually, and four cusps on the labial side. The first cusp on the labial side is the small paraconid, aligned with the protoconid distal to it. Then, a supernumerary cusp lies between the protoconid and the hypoconid, and is separated from the latter by a deep furrow. Lingually, the m2 exhibit a large metaconid (the largest cusp of the tooth), a supernumerary cusp and a smaller entoconid. In some unworn molars, the cusp on the entoconid position can be subdivided in two smaller cuspules (e.g. LIEB-PV 1169).

The m3 is the smallest molar of the row. It is wider on its mesial than on the distal end, giving a subtriangular occlusal outline. There are only two m3 assigned to this species, LIEB- PV 1156 and LIEB-PV 1169. The former is worn and the latter is almost completely unworn, showing enamel wrinkles and several cuspules on its surface. The lingual margin has a large metaconid and, distal to it, a serrated margin with four cuspules on it. The labial margin has four cusps, similar in proportion to the ones on the m2, but arranged in a curved margin, since the distal end of the tooth is narrower than the mesial one.

Measurements: Appendix S4.

Remarks: Tejedor *et al.* (2009) assigned to two different species some of the specimens here included in *H. sapoensis*: *Polydolops* sp. nov. 1 (LIEB-PV 1153) and *Polydolops* sp. nov. 2 (LIEB-PV 1173). Both were represented by maxillary fragments with M1-2, and some other specimens not explicit in that work. The differences among them consisted of a minor difference in size, and 'M1 with two lingual cusps instead of three in the posterior lobe; m1 with the second labial cusp divided and comparatively much smaller; labial accessory cusp larger than in sp nov. 2; and hypoconid of m2 more posteriorly placed and with the second lingual cusp proportionally smaller' (Tejedor *et al.*, 2009: 17). The posterior lobe of the M1 is similar in both cases. However, the specimen LIEB-PV 1153, less worn than the other, presents a small cuspule posterior to the metaconule. As previously stated, this structure cannot be seen on LIEB-PV 1173, perhaps due to the state of wear on the latter, in which the metaconule is worn, as well as the postmetaconular crista. All the other features described by Tejedor *et al.* (2009), though observable, show different states of development in all specimens, being interpreted here as part of a little instraspecific variation.

Genus *Pseudolops* Ameghino, 1902

Pseudolops Ameghinoo, 1902: 40
Polydolops Simpson, 1948: 62 [in part]
Polydolops Marshall, 1982a: 51 [in part]

Type species: Pseudolops princeps Ameghino 1902.

Included species: Only the type species.

Diagnosis: As the one for the species.

Distribution: Chubut Province, Argentina. Middle Eocene (Barrancan subage).

Pseudolops princeps Ameghino, 1902

(Fig. 7G, H, Appendix S4)
Pseudolops princeps Ameghino, 1902: 40
Polydolops princeps Simpson, 1948: 62 [in part]
Polydolops princeps Marshall, 1982: 51; fig. 41 [in part]

Lectotype: MACN-A 10332a, an isolated left P3. (Fig. 7G, H).

Emended diagnosis: Species with similar size to *Polydolops thomasi*. It differs from all known species of Polydoloopidae by having a P3 with rounded and serrated margin, not forming an angle. It differs from *Antarctodolops* spp. by having a longer and narrower P3.

Temporal and geographic distribution: The specimen comes from the Middle Eocene levels of the Gran Barranca, Chubut Province.

Measurements: Appendix S4.

Remarks: Originally, Ameghino (1902) included several specimens to define this species. Some of them are considered as pertaining to other groups now (e.g. Marshall, 1982). The syntype (MACN-A 10332a-g) included for Ameghino (1902) the following: MACN-A 10332a, an isolated left P3; MACN-A 10332b, a P3 or M1; MACN-A 10332c, an m2; MACN-A 10332d, the apex of a right inferior teeth of procumbent aspect; MACN-A 10332e, a maxillary fragment with M1-2;

MACN-A 10332f,g, two anterior portions of p3. Simpson (1948) assigned the p3 MACN-A 10332a as the lectotype of '*Polydolops*' *princeps* and referred to this species the lower incisor MACN-A 10332d, the P2, the P3, the p3m and the m2, as well as the maxillary fragment with M1-2. Later, Marshall (1982a) removed all specimens from the species except for the lectotype. The specimens are assigned as follows:

- MACN-A 10332a, a left P3 is the lectotype of *Pseudolops princeps* (Simpson, 1948).
- MACN-A 10332b, a P3 or M1 figured by Ameghino (1903). These materials were assigned to the abderitid *Abderites* by Marshall (1982); hypothesis accepted here.
- MACN-A 10332c, an isolated m2 was referred to *P. thomasi* by Simpson (1948). This designation was accepted by Marshall (1982) and in this work.
- MACN-A 10332d, apex of a lower right procumbent tooth. Marshall (1982a) accepted it as possibly belonging to a polydolopid and indicated that this tooth was the same as the one figured by Ameghino (1902) as pertaining to *Eudolops* sp. Unfortunately, this specimen could not be assigned to any genus in particular, that is why it has been remove from Pseudolops, as was proposed by Marshall (1982).
- MACN-A 10332e, a maxillary fragment with M1-2. Marshall (1982) assigned this specimen to *P. thomasi* by its overall morphology, similar to the teeth of that species. This assignment is followed here.
- MACN-A 10332f and g, two anterior portions of p3. The specimens are fragmentary and they could belong to any other polydolopid species with asymmetrical p3 (e.g. *Polydolops*).

GENUS *ANTARCTODOLOPS* WOODBURNE & ZINSMEISTER, 1984

Antarctodolops Woodburne & Zinsmeister, 1984: 916; figs 1, 2
Eurydolops Case *et al.*, 1988: 508
Polydolops Candela & Goin, 1995: 55 [in part]

Type species: Antarctodolops dailyi Woodburne & Zinsmeister, 1984.

Included species: The type species and *A. mesetaense* Chornogubsky *et al.*, 2009.

Emended diagnosis: It differs from all other known polydolopids by having two accessory cusps between the protoconid and the hypoconid on m2; it differs from all polydolopids, except *Amphidolops*, by having lower and upper molars considerably longer than wide and by having four labial cusps on the m1. It differs from *Amphidolops* by having a large lingual cusp on the anterior edge of the talonid of the m1, by the presence of at least one vertical furrow dividing labially the talonid cusps and by having better differentiated labial rows on the M1 (i.e. they have two labial rows: the stylar one and the accessory row). It differs from *Eudolops* by being smaller and having a larger p3, with larger labial and lingual ribs; they have molars with smaller and less differentiated cusps; M1 has the anterior and posterior lobes more differently sized (the latter being wider); the m3 is proportionally smaller. It differs from *Polydolops* and *Kramadolops* by the absence of p2. It differs from *Kramadolops* by having less differentiated cusps and premolars buccolingually wider.

Distribution: Marambio (Seymour) Island, Antarctic Peninsula. Early Eocene.

Remarks: Woodburne & Zinsmeister (1984) argued the presence of the p2 by the interpretation of an alveolus anterior to the p3 in the holotype. However, Chornogubsky *et al.* (2009), having at hand new and more complete materials, commented that the alveolus could not be seen, being instead a breakage in the bone.

ANTARCTODOLOPS DAILYI WOODBURNE & ZINSMEISTER, 1984

(Fig. 7I–K, Appendix S4)
Antarctodolops dailyi Woodburne & Zinsmeister, 1984: 916; figs 1, 2
Eurydolops seymourensis Case *et al.*, 1988: 508; figs 3, 4
Polydolops dailyi Candela & Goin, 1995: 55
Polydolops seymourensis Candela & Goin, 1995: 55

Holotype: UCR 20910, a right dentary fragment with p3-m2 (Fig. 7I).

Referred material: UCR 22355, an isolated left P3 (holotype of *E. seymourensis*); UCR 20911, a right dentary fragment with p3-m1; MLP 89-III-2-1, an isolated right m2; MLP 94-III-15–254, a right dentary fragment with p3-m2; MLP 95-I-10–3, an isolated left p3; MLP 96-I-5-1, an isolated right m2; MLP 96-I-5-2, an isolated right m3; MLP 96-I-5-3, a right dentary fragment with p3; MLP 96-I-5-4, a edentulous dentary fragment; MLP 88-I-1–2, a left dentary fragment with a broken m2; UCR 20912, an isolated left M1; MLP 87-II-1-1, a right maxillary fragment with P2-M1(Fig. 7J); MLP 88-I-1–4, an isolated right M1 (Fig. 7K).

Diagnosis (see: Chornogubsky et al., 2009: 291): This is the smallest species of the genus. It differs from *A. mesetaense* by having the large lingual cusp of the talonid of the m1 divided by a deep furrow; the m1 has at least three furrows that run vertically throughout its labial wall; the central labial cusp of the m2 is divided by a furrow; the lingual cusps are wider (not compressed as in *A. mesetaense*); the p3 is narrower and with a more rounded apex; the P2 is large and extremely long (not known in *A. mesetaense*); the P3 is small and with a taller crown than in other polydolopids (almost as wide as long); the M1 has more than five lingual cusps and two labial rows, the latter united by the StB, as occurres in some other polydolopids (e.g. *Pliodolops serra*). However, the more labial row becomes irregular towards the posterior margin.

Temporal and geographic distribution: All the specimens come from Early Eocene levels at Marambio (Seymour) island, Antactic Peninsula. They were exhumed from the following localities: IAA 2/95 (MLP 94-III-15–254, MLP 95-I-10–3, MLP 96-I-5-1, MLP 96-I-5-2, MLP 96-I-5-3 and MLP 96-I-5-4), DPV 2/84 (MLP 89-III-2-1), DPV 6/84 (MLP 87-II-1-1, MLP 88-I-1–4, MLP 88-I-1–2, UCR 22355, UCR 20910, UCR 20911 and UCR 20912).

Measurements: Appendix S4.

Remarks: Originally Woodburne & Zinsmeister (1984) compared this species with *Polydolops thomasi*. The number of stylar cusps is the same as observed in *P. thomasi*, but it has a lot of accessory cusps in the labialmost row. Finally, both labial rows are united anteriorly by a large StB (with the paracone fused to it; see above). Woodburne & Zinsmeister (1984) discussed if the differences among *Antarctodolops* and *Polydolops* were at the genus or species level. They compared *Polydolops* with *Amphidolops* and concluded that *Antarctodolops* had more affinities with the first, and specifically with '*Polydolops*' *serra*. However, the differences were too strong and they assigned their new species to the new genus *Antarctodolops.* Later, Goin & Candela (1995) reassigned the species to the genus *Polydolops*, because they considered that the differences were not sufficient to recognize a separate genus. New findings in the La Meseta Formation led Chornogubsky *et al.* (2009) to revalidate *Antarctodolops*, based on the features described above. This hypothesis is corroborated in the cladistic analysis presented in this work.

It was assigned to *A. dailyi* a maxillary fragment with P2-M1 with broken crowns but intact contours. Comparing the P3 of this specimen with the one from the holotype of '*E.*' *seymourensis*, it can be deduced that both P3s are indistinguishable from each other, thus being both species synonyms.

ANTARCTODOLOPS MESETAENSE CHORNOGUBSKY *ET AL.*, 2009

(Fig. 7M, N, Appendix S4)

Holotype: MLP 96-I-5–12, a right dentary fragment with p3-m3 (Fig. 7N).

Referred material: MLP 88-I-1–3, a right dentary fragment with m2; MLP 92-II-2-1, an isolated left m2; MLP 94-III-15-13a, an isolated left m1; MLP 94-III-15-13b, an isolated left m3; MLP 96-I-5–46, an isolated right m3; MLP 95-I-10–4, an isolated left M1 (Fig. 7M).

Tentatively referred material: MLP 90-I-20–4, an isolated P3.

Diagnosis (see: Chornogubsky et al., 2009 : 293): The largest species of the genus. It differs from *A. dailyi* by having the first cusp of the talonid on the m1 not divided; it has a furrow that separates the hypoconid from the cusps anterior to it; the lingual cusps of the m2 are buccolingually compressed, forming a serrated margin; the p3 is relatively longer than the one from *A. dailyi*, with a more quadrangular contour in lateral view; the P3 is large, longer and wider than the one present in *A. dailyi*; the M1 is propotionately longer, with a single lingual accessory cusp and four cusps on the StC position; the labialmost row is multicusped and close to the stylar one.

Temporal and geographic distribution: All the specimens were recorded from Early Eocene levels of Marambio Island, Antarctic Peninsula. They were recovered from the following localities: IAA 1/90 (MLP 90-I-20–4, MLP 92-II-2-1, MLP 94-III-15-13a and b, MLP 95-I-10–4, MLP 96-I-5–12 and MLP 96-I-5–46) and DPV 6/84 (MLP 88-I-1–3).

Measurements: Appendix S4.

ANTARCTODOLOPS SP.

(Fig. 7L, Appendix S4)

Referred material: UCR 20913, an isolated left M2 (Fig. 7L).

Temporal and geographic distribution: The specimen was exhumed from the Early Eocene levels of the La Meseta Formation (Marmbio Island, Antarctic Peninsula) from the locality DPV 6/84.

Measurements: Appendix S4.

Remarks: Even though this molar has the proportions and general features of an M2, the presence of a complete stylar row makes it uncommon. As was previously commented by Chornogubsky *et al.* (2009), and based on its size, this tooth could be better assigned to *A. dailyi* than to *A. mesetaense*. However, the presence of two supernumerary cusps in the StC position (one more than in *A. dailyi*) suggest that, in spite of its small size, it could be also assigned to *A. mesetaense*. These mixed features led Chornogubsky *et al.* (2009) to assign this material to the genus but not to any species. This view is shared here.

Genus Amphidolops Ameghino, 1902

Amphidolops Ameghino, 1902: 42
Anadolops Ameghino, 1903: 186
Seumadia Simpson, 1935a: 5

Type species: Amphidolops serrula Ameghino, 1902.

Included species: The type species, *A. yapa*, *A. minimus* sp. nov. and *A. intermedius* sp. nov.

Diagnosis: The species of this genus are characterized by having numerous cusps and strong enamel crenulations ('wrinkles') in their molars. The genus differs from the others, except *Antarctodolops*, by having two rows of labial cusps on the M1, which are at the same level in the crown, and are almost or completely over-imposed; also, by having a proportionally long m1. It differs from *Pliodolops* by having lower molars with aligned hypoconid and entoconid. It differs from *Kramadolops*, *Eudolops* and *Polydolops* by having poorly differentiated cusps.

Temporal and geographic distribution: Patagonia, Argentina. Early Palaeocene to Middle Eocene (Paso del Sapo fauna and Casamayoran SALMA).

Remarks: In the past, Simpson (1948) and Marshall (1982) observed the crenulations on the occlusal surface of the molar enamel as a diagnostic feature for the genus. This character is not exclusive, being present in most polydolopid molars that show no wear; however, the crenulations could be deeper in the species of *Amphidolops*, reaching the margins of the occlusal surface of the molars in some species.

Amphidolops serrula Ameghino, 1902

(Fig. 8A, B, Appendix S4)
Amphidolops serrula Ameghino 1902: 42
Anadolops thylacoleoides Ameghino, 1903: 186; fig. 120

Holotype: MACN-A 10357, an isolated left m2 (Fig. 8A).

Referred material: MACN-A 10339, a left dentary fragment with m1-3 (holotype of *Anadolops thylacoleoides*); AMNH 28922, an isolated right m1; AMNH 28933, an isolated left m1; AMNH 28923, an isolated left M2; AMNH 28929, a left maxillary fragment with M1-2 (Fig. 8B); MLP 66-V-4–25 a left dentary fragment with a broken m1; MLP 59-II-28–86, a right maxillary fragment with M1-2; AMNH 28438, an isolated right M1.

Emended diagnosis: Characterized by having a great number of cuspules and crenulations in their upper and lower molars, comparable with the ones of the other species of the genus, but larger. It differs from *A. minimus* by having upper molars with two rows of labial cusps and not one. These two rows are less defined when compared with *A. intermedius*.

Temporal and geographic distribution: All specimens referred to this species were exhumed from the Middle Eocene levels of Patagonia, Argentina. In particular, the holotype and AMNH 28438 come from Gran Barranca. AMNH 28933, AMNH 28922, AMNH 28923 and AMNH 28929 come from Rinconada de los Lopez. MLP 59-II-28–86 and MLP 66-V-4–25 were recorded from Laguna de la Bombilla. The specimen MACN-A 10339, described by Ameghino (1902), was recovered from the '*Couches à Notostylops*'.

Measurements: Appendix S4.

Remarks: The holotype and only referred material of *Anadolops thylacoleoides* Ameghino, 1902 (MACN-A 10339) corresponds to a mandibular fragment with m1-m3 that was interpreted by Ameghino as having m4-m6 [p3-m2]. That is why he considered that it has no m7 [m3] and that the m4 [p3] did not form a cutting crest, but had a wide crown. These observations justified the recognition of a new genus. However, Simpson (1948) recognized that the supposed p3 was really an m1, and he synonymized the species with *Amphidolops serrula*. The holotype of the latter (MACN-A 10357; Fig. 8A) corresponds to an isolated, unworn m2, the only material in the original description of the species (Ameghino, 1902). The L/W ratio is 1.75. The m2 belonging to '*Anadolops thylacoleoides*' is similar to the former, but is a little larger and with a L/W ratio of 1.6. Marshall (1982) recognized that the worn specimen MACN-A 10357 should have cuspules and crenulations, that may give the molar serrated anterior and posterior margins. The same is considered in this study, thus being both species synonyms.

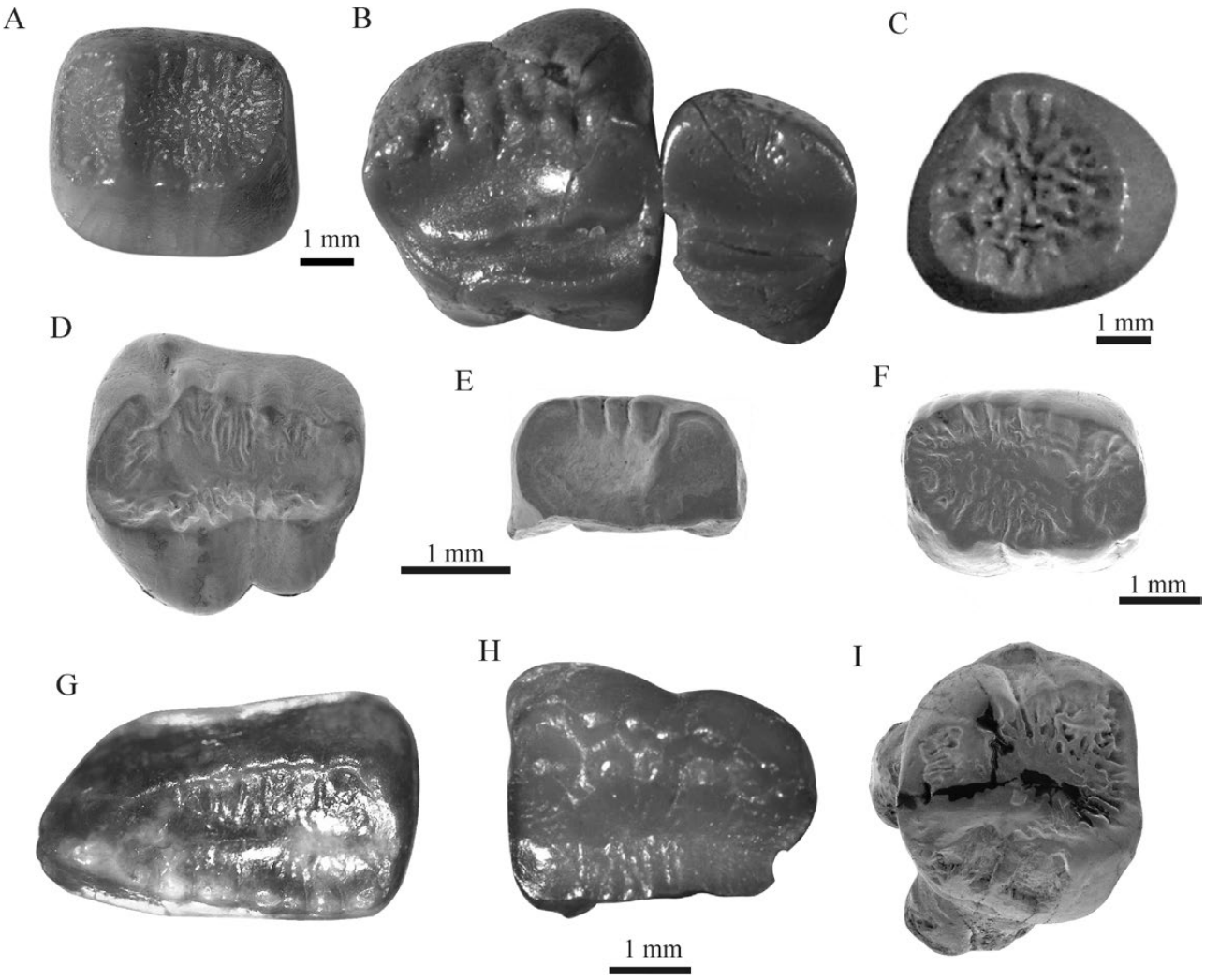

Figure 8. A, B, *Amphidolops serrula*. A, left m2 from the holotype (MACN-A 10357). B, left M1-2 (AMNH 28929, cast). C, *Amphidolops yapa*. Right M3 from the holotype (AMNH 28431, cast). D, E, *Amphidolops minimus*. D, right M1, holotype (LIEB-Pv 1170). E, right m2 (LIEB-Pv 1172). F–I, *Amphidolops intermedius*. F, right m2, holotype (LIEB-Pv 1187). G, right m1 (LIEP-Pv 1183). H, right M1 (LIEB-Pv 1179). I, right M2 (LIEB-Pv 1182). All specimens in occlusal view.

The m1 AMNH 28922 and AMNH 28933 were assigned to this species because of their proportions, being considerably longer than wide, and because of the presences of stark enamel wrinkles, as well as small labial and lingual cusps. The upper molars were assigned to the species [as they were also by Simpson (1948) and Marshall (1982)] due to the presence of structures expected for the occlusal antagonists of the lower teeth mentioned above.

AMPHIDOLOPS YAPA (SIMPSON, 1935B)

(Fig. 8C)

Seumadia yapa Simpson 1935b: 6; fig. 3

Amphidolops yapa Marshall, 1982: 55; fig. 42; 56; fig. 43

Holotype: AMNH 28431, an isolated left M3 (Fig. 8C).

Emended diagnosis: Large species of *Amphidolops*, with strongly wrinkled enamel. the recognizable cusps are weak and the trigon basing is shallow, even more than expected for other species of the genus.

Temporal and geographic distribution: The only known material has been recorded in the Early Palaeocene levels of Peñas Coloradas Formation at Cerro Redondo locality in Chubut Province.

Measurements: Appendix S4.

Remarks: Amphidolops yapa was first described by Simpson (1935b), who recognized the new species *Seumadia*, different from *Amphidolops*, by having lower margins on the M3 than the ones expected for

Amphidolops. Marshall (1982) considered *Seumadia* as a synonym of *Amphidolops* because the differences were not enough to create a new genus.

About the location of the type specimen, Simpson (1935a, b) commented that it came from levels that may corresponds to the 'Río Chico Formation, 37 meters above the "Banco Verde" of the Salamanca, Cerro Redondo, west of Puerto Visser, Chubut, Argentina' (Simpson 1935b: 6).

The type specimen is a M3, as previously mentioned. Even though it is poorly informative, it could be assignable to *A. serrula* by having a surface filled with crenulations, as well as by having two wide and low cusps in its labial and lingual margins. However, it is a little larger than expected for that species (the M3 is not known in *A. serrula*). Finally, due to the features mentioned by Simpson (1935b), as well as the poorly informative nature of the M3, and because it was recorded in much older levels, *Amphidolops yapa* is here accepted as a valid species.

AMPHIDOLOPS MINIMUS SP. NOV.

(Fig. 8D, E, Appendix S4)
***Amphidolops* sp. nov. 1** Tejedor *et al.* 2009: 18

Zoobank registration: urn:lsid:zoobank.org:act:6B067B58-9285-436B-B4DB-658102E4A436

Holotype: LIEB-PV 1170, an isolated right M1 (Fig. 8D).

Referred material: LIEB-PV 1172, an isolated right m2 (Fig. 8E); LIEB-PV 1171, an isolated left M1.

Etymology: From Latin *minimus*, least, because it is the smallest species of the genus.

Diagnosis: It differs from the other species of the genus by its smaller size, and by the absence of ectoflexus and a second labial row on the M1. It differs from *A. serrula* by having the M1 proportionately shorter and with a wider stylar area, because the cusps occupy a more lingual position. The most posterior labial cusp is higher than the others. The metacone on the M1 is more anteriorly placed, more anterior than the last stylar cusp. The m2 has a longer metaconid and the talonid cusps are more individualized. It differs from *Amphidolops intermedius* by the presence of a single labial cusp row on the M1 and by the fewer lingual cusps on the m2.

Description: The holotype corresponds to a wider than long isolated M1, with its trigon basin presenting enamel wrinkles. Lingually, the tooth has two lobes: the mesial one, smaller and with the paraconule and a small cuspule distal to it. The distal lobe has a small protocone and metaconule and a small cuspule distal to the latter. Anterior to the protocone, a few wrinkles end on the lingual border of the tooth forming some cusp-like crenulations. Labially, the molar exhibits one cusp row with five cusps on it. Mesially, the paracone + StB, then two cusps on the StC position, a similarly sized StD and a large StE. The metacone is connected to both, the StD and the StE, but is more aligned to the latter. On the labial margin, a small cusp lies between the StD and the StE, almost aligned to the metacone. The specimen LIEB-PV 1170 corresponds to another isolated M1, similar to the holotype, but more crenulated and with a third cuspule on the StC position. As a result, the three 'StC' are smaller than the other stylar cusps.

Assigned to this species is the lingual half of the m2 LIEB-PV 1172. This tooth shows some wear and, perhaps because of that, no enamel wrinkles can be seen on its basin. However, the lingual border is well preserved, showing a wide metaconid and four cusps distal to it. The first three are subequal in height. The last one, the entoconid, is wider and crest-like. All the cusps are divided by vertical labial furrows.

Temporal and geographic distribution: All specimens come from the Middle Eocene levels of the Tufolitas Laguna del Hunco Formation at Laguna Fría locality.

Measurements: Appendix S4.

Remarks: The upper teeth were assigned to this species due to their morphology, coherent with the one expected for the occlusal antagonists of the holotype: the same degree of the extreme labial and lingual position of the cusps is observed in the upper molar. Moreover, the size of the specimens is compatible with the one of the holotype.

AMPHIDOLOPS INTERMEDIUS SP. NOV.

(Fig. 8F–I, Appendix S4)
Amphidolops sp. nov. 2 Tejedor *et al.* 2009: 18

Zoobank registration: urn:lsid:zoobank.org:act:1010F487-92EF-415E-B441-B95711A93FD2

Holotype: LIEB-PV 1187, an isolated right m2 (Fig. 8F).

Referred material: LIEB-PV 1188, an isolated left m2; LIEB-PV 1179, an isolated and broken right M1 (Fig. 8H); LIEB-PV 1180, an isolated right M2; LIEB-PV 1181, an isolated right M2; LIEB-PV 1182, an isolated right M2 (Fig. 8I); LIEB-PV 1183, an isolated right m1 (Fig. 8G); LIEB-PV 1184, an isolated left m1; LIEB-PV 1185, an isolated left m2; LIEB-PV

1186, an isolated right m2; LIEB-PV 1189, an isolated right m?1; LIEB-PV 1190, an isolated right m2.

Etymology: From the Latin *intermedius*, in between, because it is intermediate in size between the smallest (*A. minimus*) and the larger (*A. yapa* and *A. serrula*) species.

Diagnosis: Species of *Amphidolops* smaller than *A. serrula* and *A. yapa*, and larger than *Amphidolops minimus*. The m2 has more defined cusps than the former but less defined than the latter. Unlike *A. serrula*, the wrinkles in this molar are less irregular and poorly anastomosed. In the M1 there are two labial rows of cusps, better defined than in *A. serrula* (*A. minimus* has only one row of labial cusps) and, like it, has a well-developed extoflexus (absent on *A. minimus*).

Description: Several first and second lower and upper molars have been assigned to these species. The m1 is much longer than wider and subtriangular in occlusal view. It shows the typical features of the genus: a reduced trigonid, only formed by the protoconid, and a long multicuspid talonid. The labial and lingual margins show several poorly differentiated cuspules, seven lingually and five or six labially. The talonid basin exhibits transverse crenulations or enamel wrinkles.

The m2 is much shorter than the m1, even though it is longer than wider. It is similar to the one from *A. serrula*, but much smaller and its crenulations are not so developed as in that species and in *A. yapa*. The lingual border of the tooth is serrated, since the metaconid is larger and buccolingually compressed, and the four or five cusps that follow it are small, also compressed and separated by labial furrows. Labially, four or five cusps can be seen: the paraconid, the protoconid, a supernumerary cusp, the hypoconid and a small cuspule is present in unworn specimens. Since the crenulations reach the margins of the tooth, it appears to have crenulations on them.

Only one M1 has been preserved and it is broken on its lingual side. Labially, it shows two cusp rows united by the StB and, mesiolingually, by the relictual paracone. The stylar row includes also four cusps. Two 'StC', the StD and the StE. The latter is conical in shape. The metacone is small, equidistant to the StD and StE, and united to them by two crests. The external labial row, formed by six supernumerary cusps, is irregular, since an ectoflexus is below the third supernumerary cusp. The last two cusps are small and near each other on a curved crest.

As in *A. serrula*, the M2 is much smaller than the M1, quadrangular in occlusal shape and almost as long as wide. The least worn M2 preserved is LIEB-PV 1182, which shows stark crenulations, but the lingual margin is partly broken. This straight margin is best preserved on LIEB-PV 1180 and LIEB-PV 1181, where three cusps can be seen: the paraconule (mesial), a small protocone (central) and the metaconule (distal). Labially, the teeth show three stylar cusps: StB, StC and StD. Distally, a vestigial StE can be seen on LIEB-PV 1182. In the latter, a small paracone is present fused to the labial wall of the StB. The StC is the smallest of the stylar cusps, but is a little larger on LIEB-PV 1180. The StD is the larger cusp of the row and the metacone is partially fused to its lingual wall. At the labial margin a well-defined cusp is positioned below the StC.

Temporal and geographic distribution: All specimens come from the Middle Eocene levels of the vicinity from Paso del Sapo, Chubut Province. In particular, specimens LIEB-PV 1179, LIEB-PV 1180, LIEB-PV 1189 and LIEB-PV 1190 were exhumed from levels of the Tufolitas Laguna del Hunco Formation at Laguna Fría locality. Specimens LIEB-PV 1187, LIEB-PV 1188, LIEB-PV 1181, LIEB-PV 1182, LIEB-PV 1183, LIEB-PV 1184, LIEB-PV 1185 and LIEB-PV 1186 were recorded from levels of the Andesitas Huancache Formation at La Barda locality.

Measurements: Appendix S4.

GENUS *PLIODOLOPS* AMEGHINO, 1902

Pliodolops Ameghino, 1902: 41
Polydolops Ameghino, 1902: 39 [in part]
Anissodolops Ameghino, 1903: 148

Type species: Pliodolops primulus Ameghino, 1902.

Included species: The type species, *P. rothi* (Simpson, 1936), *P. kamektsen* (Simpson, 1935) and *P. winecage* (Simpson, 1935).

Diagnosis: Polydolopids of variable size, from small (*P. kamektsen*) to comparable to *Polydolops thomasi* (*P. rothi*). They differ from the rest of polydolopids by having lower molars with the hypoconid more anteriorly positioned than the entoconid, particularly on the m2. They differ from the species of *Amphidolops* and *Antarctodolops* by having fewer labial cusps on the m1 and lingual cusps on the m2. They differ from the species of *Eudolops*, *Kramadolops* and *Polydolops* by having cusps usually less differentiated (i.e. fused at the base). They differ from the species of *Hypodolops*, *Antarctodolops* and *Amphidolops* by having only one cusp on the StC position and the paracone on M1 partially fused with the StB.

Distribution: Patagonia, Argentina. Early to Middle Eocene (Itaboraian to Casamayoran SALMAs).

PLIODOLOPS PRIMULUS AMEGHINO, 1902 COMB. NOV.

(Fig. 9A–D, Appendix S4)
Pliodolops primulus Ameghino, 1902: 41
Polydolops serra Ameghino, 1902: 39
Polydolops primulus Simpson, 1948: 62
Polydolops bocurhor Simpson, 1948: 62; pl. 6; figs 1, 2 [in part]
Amphidolops serrifer Ameghino, 1902: 42
Anissodolops serrifer Ameghino, 1903: 148; fig. 72

Lectotype: MACN-A 10341, a left dentary fragment with p2-3 and broken m1 (Fig. 9A).

Paralectotype: MACN-A 10361, a right dentary fragment with m1-2 (Fig. 9B); MACN-A 10363, a left dentary fragment with m2-3.

Holotype: MACN-A 10353, a fragment of right maxillary fragment with M1-2 (Fig. 9D).

Referred material: MACN-A 10341, a left dentary fragment with p2-3 and broken m1 (lectotype of Polydolops serra; Fig. 9A); MACN-A 10361, a right dentary fragment with m1-2 (Fig. 9B); MACN-A 10363, a left dentary fragment with m2-3; MACN-A 10359, an isolated right m2 (holotype of *Amphidolops serrifer*); AMNH 28412, an isolated right M1; AMNH 28885, an isolated right M3; AMNH 28427, a right maxillary fragment with M1-2 (holotype of *Polydolops bocurhor*); LIEB-PV 1213, an isolated left m2; LIEB-PV 1215, an isolated left m2, LIEB-PV 1216, an isolated left m3; LIEB-PV 1220, an isolated right m3; LIEB-PV 1221, a right dentary fragment with broken m1-2 rotos and a complete m3; LIEB-PV 1222, a right dentary fragment with broken m2 and complete m3; LIEB-PV 1225, an isolated left m1; LIEB-PV 1233, a right dentary fragment with p3-m3; LIEB-PV 1235, an isolated right m2; LIEB-PV 1239, an isolated right m1; LIEB-PV 1227, a left maxillary fragment with M1-2; LIEB-PV 1161, an isolated left m?3; LIEB-PV 1162, an isolated right m2; LIEB-PV 1191, a left maxillary fragment with los M1-2 (Fig. 9C); LIEB-PV 1192, an isolated left M1; LIEB-PV 1193, an isolated left M1; LIEB-PV 1194, an isolated left M2; LIEB-PV 1195, an isolated left M3; LIEB-PV 1196, an isolated right M3; LIEB-PV 1197, an isolated left M1; LIEB-PV 1198, an isolated left M1; LIEB-PV 1199, an isolated left M2; LIEB-PV 1200, an isolated right M1; LIEB-PV 1202, an isolated right M1; LIEB-PV 1203, an isolated right M1; LIEB-PV 1204, an isolated right M1; LIEB-PV 1205, an isolated right M1; LIEB-PV 1206, an isolated right M2; LIEB-PV 1207, an isolated right M2; LIEB-PV 1208, an isolated right M2; LIEB-PV 1209, an isolated right M2; LIEB-PV 1211, an isolated left M3; LIEB-PV 1212, a left dentary fragment with a broken m1, complete m2, and roots of m3; LIEB-PV 1228, an isolated left M1; LIEB-PV 1230, an isolated left M2; LIEB-PV 1231, an isolated left M1; LIEB-PV 1232, an isolated left M1; LIEB-PV 1244, an isolated, broken right M1; AMNH 28408, an isolated and broken right m2; AMNH 28409, an isolated right M1; AMNH 28425, an isolated right M1; AMNH 28426, an isolated left M1.

Tentatively referred material: AMNH 28429, an isolated right m1.

Emended diagnosis: It differs from the other species of the genus by having a proportionately longer m2 with its lingual cusps more bucollingually compressed, as well as by the presence of a more buccolingually compressed M2. It differs from *P. winecage* by the larger size and greater development of the cusps on the m1. It differs from *P. rothi* by having a extremely wide p3, with the anterior root much smaller than the posterior one and more labially positioned in the dentary, thus having a labial rib that is positioned almost forwardly positioned.

Temporal and geographic distribution: All specimens come from levels of the Middle Eocene of Patagonia, Argentina. The specimen MACN-A 10341 and MACN-A 10361 have no more data than belonging to the '*Couches à Notostylops*' (Ameghino, 1902). Specimens MACN-A 10353, MACN-A 10359, and MACN-A 10363 were recovered from Gran Barranca. The specimen AMNH 28412 was exhumed from the proximity of Cabeza Blanca. Specimen AMNH 28429 was exhumed from Cañadón Vaca, and AMNH 28885 from Lomas Blancas; specimens AMNH 28408 and AMNH 28409 were recovered from the vicinity of Cabeza Blanca. Material AMNH 28425, AMNH 28426 and AMNH 28427 were exhumed from Cañadón Vaca. Finally, the specimens LIEB-PV come from two localities with Middle Eocene levels near Paso del Sapo locality: (1) LIEB-PV 1161, LIEB-PV 1162; LIEB-PV 1212; LIEB-PV 1213, LIEB-PV 1214; LIEB-PV 1215, LIEB-PV 1216, LIEB-PV 1218, LIEB-PV 1219, LIEB-PV 1220, LIEB-PV 1233, LIEB-PV 1234, LIEB-PV 1235, LIEB-PV 1236, LIEB-PV 1237, LIEB-PV 1227, LIEB-PV 1244; LIEB-PV 1191, LIEB-PV 1192, LIEB-PV 1193, LIEB-PV 1194, LIEB-PV 1195, LIEB-PV 1196, LIEB-PV 1228 and LIEB-PV 1230 were recovered from levels of the Tufolitas Laguna del Hunco Formation at Laguna Fría; and (2) LIEB-PV 1221, LIEB-PV 1222, LIEB-PV 1223, LIEB-PV 1224, LIEB-PV 1225, LIEB-PV 1226, LIEB-PV 1238, LIEB-PV 1239, LIEB-PV 1197, LIEB-PV 1198, LIEB-PV 1199, LIEB-PV 1200, LIEB-PV 1202, LIEB-PV 1203, LIEB-PV 1204,

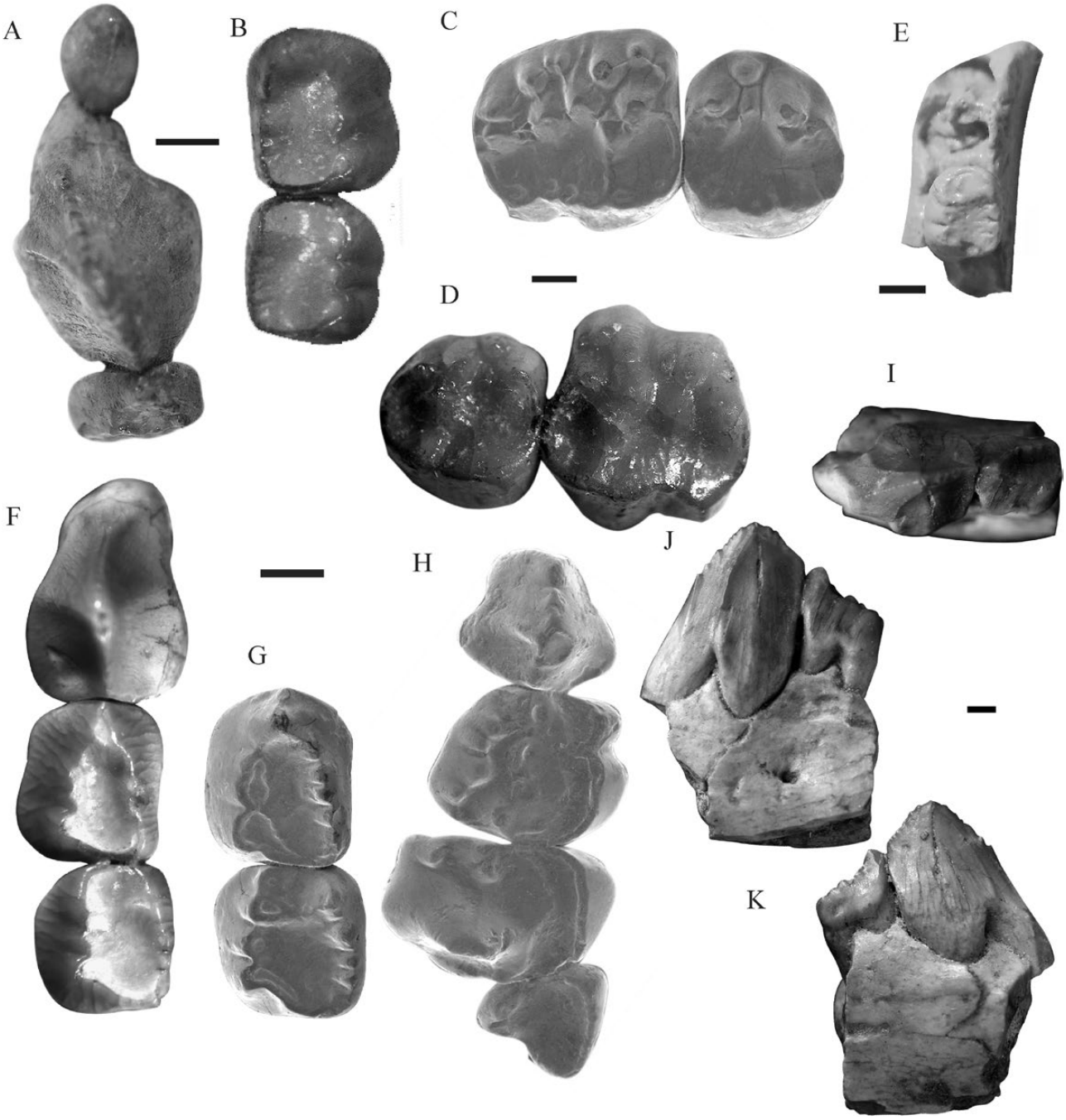

Figure 9. A–D, *Pliodolops primulus*. A, left p2-p3 and trigonid of m1 (MACN-A 10341). B, right m1-2 (MACN-A 10361). C, left M1-2 (LIEB-PV 1191). D, right M1-2 from the holotype (MACN-A 10353). All specimens in occlusal view. E, *Pliodolops kamektsen*. A left dentary fragment with a broken m2 from the holotype (AMNH 28525, cast) in occlusal view. F–H, *Pliodolops rothi*. F, left p3-m2 from the holotype (MLP 11–122). G, left m1-2 (LIEB-Pv 1267). H, right P3-M3 (LIEB-Pv 1252). All specimens in occlusal view. I–K, *Pliodolops winecage*. Left p3-m1 izquierdos from the holotype (AMNH 27893). I, occlusal view. J, labial view. K, lingual view. Scale bar = 1 mm.

LIEB-PV 1205, LIEB-PV 1206, LIEB-PV 1207, LIEB-PV 1208, LIEB-PV 1209, LIEB-PV 1210, LIEB-PV 1211, LIEB-PV 1231 and LIEB-PV 1232 come from levels of the Andesitas Huancache Formation at La Barda.

Measurements: Appendix S4.

Remarks: When Ameghino (1902) first recognized *Pliodolops primulus* he described in detail two upper

molars, that later he figured (Ameghino, 1903; fig. 27). Simpson (1948) considered that the features on this specimen where typical for the species of *Polydolops*, then consider it as *Polydolops primulus*. Was Marshall (1982) who synonymized *P. primulus* to *Polydolops serra*, represented originally by three mandibular fragments (Ameghino, 1902; Simpson, 1948). Here, since the genus Pliodolops is revalidated, and *P. primulus* and *P. serra* were erected at the same time (Ameghino, 1902), the valid species should be *Pliodolops primulus*.

The specimens AMNH 28425, AMNH 28426 and AMNH 28427 were originally assigned to *Polydolops bocurhor* by Simpson (1948). This species is solely based on upper dentition. Marshall (1982) considered that *Polydolops bocurhor* was a synonym of *Polydolops serra*, a species only based on lower dentition. Marshall (1982) also considered that *Polydolops primulus*is a synonym of *P. serra*. This opinion is followed here.

The specimen AMNH 28429 is a right isolated m1 originally assigned by Simpson (1948) to *P. serra*. However, it possesses some differences with the other m1 assigned to this species: lingually, the large cusp is bigger than the others (similar in proportion to the one present in *P. thomasi*); behind it there are two smaller, similar cusps, and the protoconid is tall and does not show crenulations in its crests. Even though these differences seem important, there is an overall similarity with the other ones here referred to *P. primulus*, that is why it is doubtfully referred to this species.

The specimens labeled as *Polydolops serra* MACN-A 10355 corresponds to two posterior fragments of edentulous dentaries that were not included in the studies of Simpson (1948) and Marshall (1982). They both come from beds of *Notostylops* at Gran Barranca and have a size comparable with the one of *P. primulus* (although also with other species, such as *P. rothi*). Moreover, both dentaries have three completely preserved alveoli corresponding to the m3 and the alveolus of the posteriormost root of the m2. One of them has the last alveolus smaller than the anterior, a feature observed in Polydolopidae, where the m3 is narrower posteriorly, but no further assignation could be made. The second dentary has the last two alveoli of the same size, thus probably not belonging to a polydolopid.

Finally, several specimens with upper dentition assigned to *P. rothi* by Tejedor *et al.* (2009) are here assigned to *P. primulus*, understanding that some intraspecific variation occurs on the posterolabial quadrant of the M2 (see Fig. 9C), where the StE is smaller and the metacone could be mostly fused to the StD, or having a better developed StE and a more distinct metacone (Fig. 9D).

PLIODOLOPS KAMEKTSEN (SIMPSON, 1935) COMB. NOV.

(Fig. 9E, Appendix S4)
?*Polydolops kamektsen* Simpson, 1935b: 5; fig. 2
Polydolops kamektsen Marshall, 1982: 20; figs 13, 14

Holotype: AMNH 28525, a left dentary fragment with alveoli from m1 and complete m2 (Fig. 9E).

Diagnosis: *Pliodolops* species of small size (smaller than *P. rothi*); m2 with hypoconid more anteriorly projected than the entoconid [modified from Marshall (1982)].

Temporal and geographic distribution: The specimen comes from the Early Eocene levels of Cañadón Hondo locality at Chubut Province.

Measurements: Appendix S4.

PLIODOLOPS ROTHI (SIMPSON, 1936) COMB. NOV.

(Fig. 9F–H, Appendix S4)
Polydolops rothi Simpson, 1936: 71; fig. 1
Polydolops bocurhor Simpson, 1948: 62; pl. 6; figs 1, 2 [in part]
Polydolops primulus Simpson, 1948: 62 [in part]
Polydolops unicus Tejedor *et al.*, 2009: 14; fig. 4

Holotype: MLP 11–122, a left dentary fragment with p3-m2 (Fig. 9F).

Referred material: LIEB-PV 1214, an isolated left m2; LIEB-PV 1218, an isolated right m2; LIEB-PV 1223, an isolated right m1; LIEB-PV 1224, an isolated left m1; LIEB-PV 1226, an isolated left m1; LIEB-PV 1234, an isolated right m2; LIEB-PV 1236, an isolated left m1; LIEB-PV 1237, an isolated left m1; LIEB-PV 1252, a right maxillary fragment with P3-M3 (holotype of *P. unicus*) (Fig. 9H); LIEB-PV 1240, a left maxillary fragment with M2-3; LIEB-PV 1241, an isolated left M1; LIEB-PV 1242, an isolated right M1; LIEB-PV 1243, an isolated right M1; LIEB-PV 1245, a left maxillary fragment with M1-2; LIEB-PV 1246, an isolated left M1; LIEB-PV 1247, an isolated left M2; LIEB-PV 1248, an isolated left M2; LIEB-PV 1249, an isolated left M2; LIEB-PV 1250, an isolated left M2; LIEB-PV 1251, a right maxillary fragment with P3-M3; LIEB-PV 1253, an isolated right M1; LIEB-PV 1254, an isolated right M1; LIEB-PV 1255, an isolated right M1; LIEB-PV 1256, an isolated right M2; LIEB-PV 1257, an isolated right M3; LIEB-PV 1258, an isolated right M3; LIEB-PV 1217, a right dentary fragment with m1-3; LIEB-PV 1259, a left dentary fragment with m1-2 and roots of del p3; LIEB-PV 1260,

a left dentary fragment with m2-3; LIEB-PV 1261, an isolated left m2; LIEB-PV 1262, a right dentary fragment with m1-2; LIEB-PV 1263, a left dentary fragment with m1-2; LIEB-PV 1264, an isolated right m2; LIEB-PV 1265, an isolated left m2; LIEB-PV 1266, an isolated, broken m2; LIEB-PV 1267, a right dentary fragment with broken p3, complete m1-2, and roots of m3 (Fig. 9G); LIEB-PV 1268, a right dentary fragment with m2; LIEB-PV 1269,a right dentary fragment with m2; LIEB-PV 1270, a right dentary fragment with m2; LIEB-PV 1271, a right dentary fragment with broken m1 roto, complete m2, and roots of m3; LIEB-PV 1272, an isolated left m1; LIEB-PV 1273, an isolated right m1; LIEB-PV 1274, an isolated right m1; LIEB-PV 1275, an isolated right m2; LIEB-PV 1276, an isolated right m2; LIEB-PV 1277, an isolated right m3; LIEB-PV 1278, an isolated right m3.

Emended diagnosis: Polydolopids similar in size to *Polydolops thomasi*, although a little smaller and with more robust maxilla; the M1 is proportionately shorter; it differs from other polydolopids by having the M2 much wider than long (even wider than the M1), and with metacone and StD fused and hypertrophied in such a way that the resultant cusp protrudes ventrally below the occlusal plane of the molar series; it differs from *P. primulus* in having a hypoconid much more forwardly positioned in the lower molars than the hypoconid. It differs from other species of the genus by the following combination of features: little or moderately developed p3, with the anterior margin steeper than the posterior one and having a small cusp in the anterior crest of the protoconid on the m1 (not visible in all specimens)

Temporal and geographic distribution: All specimens come from the middle levels of the Chubut Province. The holotype was exhumed from Middle Eocene levels in the proximity of Gaiman. The specimens LIEB-PV come from two localities with Middle Eocene levels near Paso del Sapo locality: (1) LIEB-PV 1214; LIEB-PV 1218, LIEB-PV 1234, LIEB-PV 1236, LIEB-PV 1237, LIEB-PV 1240, LIEB-PV 1241, LIEB-PV 1242, LIEB-PV 1243, LIEB-PV 1217, LIEB-PV 1259, LIEB-PV 1260, LIEB-PV 1261 and LIEB-PV 1262 were recovered from levels of the Tufolitas Laguna del Hunco Formation at Laguna Fría; and (2) LIEB-PV 1223, LIEB-PV 1224, LIEB-PV 1226, LIEB-PV 1245, LIEB-PV 1246, LIEB-PV 1247, LIEB-PV 1248, LIEB-PV 1249, LIEB-PV 1250, LIEB-PV 1251, LIEB-PV 1252; LIEB-PV 1253, LIEB-PV 1254, LIEB-PV 1255, LIEB-PV 1256, LIEB-PV 1257, LIEB-PV 1258, LIEB-PV 1263, LIEB-PV 1264; LIEB-PV 1265, LIEB-PV 1266, LIEB-PV 1267, LIEB-PV 1268, LIEB-PV 1269, LIEB-PV 1270, LIEB-PV 1271, LIEB-PV 1272, LIEB-PV 1274, LIEB-PV 1275, LIEB-PV 1276, LIEB-PV 1277 and LIEB-PV 1278 come from levels of the Andesitas Huancache Formation at La Barda.

Measurements: Appendix S4.

Remarks: In the original diagnosis of '*Polydolops*' *rothi*, Simpson (1936) commented that the p3 (m1 in its nomenclature) had smooth crenulations in its cutting edge, while Marshall (1982) did not observed them. Due to the wear of the tooth, the crenulations are difficult to see; however, they are present.

Because this species was only found in the Paso del Sapo Fauna, and due to its relative abundance and specialized features, *Pliodolops unicus*, was suggested to be used as part of the definition of that association by Tejedor *et al.* (2009).

A new analysis of the specimens pertaining to *P. primulus*, *P. rothi* and *P. unicus* made clear that *P. unicus* is the junior synonym of *P. rothi*, since the mesial projection of the hypoconid on the m2 is well developed on the type of *P. rothi*, even though is a little masked by the wear of the tooth (see Fig. 9F and 9G where a worn and unworn m2 can be seen). Moreover, some intraspecific variation can be seen on this projection. On the other hand, the upper molars now assigned to *P. primulus* show also some variation on the development of the metacone (see above), although this cusp is always less developed than on *P. rothi*.

PLIODOLOPS WINECAGE (SIMPSON, 1935) **COMB. NOV.**

(Fig. 9I–K, Appendix S4)

Polydolops winecage Simpson, 1935b: 4; fig. 1

Holotype: AMNH 27893, a left dentary fragment with p3-m1 (Fig. 9I–K).

Emended diagnosis: Middle-sized polydolopid, with a p3 much larger than the m1. Similar to *P. rothi* and *P. primulus* by having the hypoconid anteriorly positioned, but it differs from them in the proportions of the p3, much higher and buccolingually wider in *P. winecage*.

Temporal and geographic distribution: The only known specimen comes from the Middle Eocene levels of Bajo de la Palangana locality, Chubut Province.

Measurements: Appendix S4.

Remarks: The original material of *P. winecage* is included in the collection of the Geology and Paleontology Museum, University of Padua (Italy) but does not have a number. Simpson (1935b), who worked with a cast of that specimen, used the number of the cast, AMNH 27893. This number was used in this work as well.

GEN. ET SP. INDET. 1

(Fig. 10A)

Referred material: MLP 77-VI-14–5, a right maxillary fragment with P2-M2 (Fig. 10A); AMNH 28437, an isolated left M3.

Temporal and geographic distribution: Both specimens were collected from Middle Eocene levels at Gran Barranca, Chubut Province, Argentina.

Remarks: The maxillary fragment with P2-M2 MLP 77-VI-14–5 and the isolated M3 AMNH 28437 previously assigned to *E. tetragonus* by Marshall (1982) are here considered as indeterminate, since the molars have strong differences with the holotype of *E. tetragonus*, having an M1 with more and proportionally smaller cusps, and the metacone only partially fused with the base of StE (completely fused and hypertrophied in *E. tetragonus*). The stylar cusps StB and StC are not aligned (i.e. StB is more lingually placed than StC), and present a well-developed ectoflexus (this is not seen in the holotype or in the lower teeth).

GEN. ET SP. INDET. 2

(Fig. 10B–D, Appendix S4)

Polydolops sp. nov. 3 Tejedor *et al.*, 2009

Referred material: LIEB-PV 1178, a right dentary fragment with alveolus of the p2 and complete p3-m1 (Fig. 10B–D).

Temporal and geographic distribution: The specimen comes from the vicinity of Paso del Sapo locality, Chubut Province, from levels of the Andesitas Huancache Formation at La Barda. Middle Eocene (Paso del Sapo Fauna).

Measurements: Appendix S4.

Remarks: The specimen LIEB-PV 1178 was originally assigned to the genus *Polydolops* (*Polydolops* sp. nov. 3 Tejedor *et al.* 2009). In the description, Tejedor *et al.* (2009) commented that it has a mosaic of features considering *P. thomasi* and '*P.*' *mayoi*, some of them generalized, and other more derived. Some differences include having a large p2, when compare with other polydolopids, a stark difference in size of the p3 and m1. The size difference among the p3 and the m1 is more marked than in any other polydolopid, but the presence of a quadrangular m1 with small lingual and labial cuspules is common to other species, particularly of *Amphidolops* and *Pliodolops*. The proportions and cusp development of the m1 is observable in *P. winecage*, though the latter is much smaller in absolute size. The proportions and cusp development of the m1 is observable in *P. winecage*, though the latter is much smaller in absolute size and the premolar is much more robust when compared to the mesiodistally shortened but tall p3 of LIEB-Pv 1178. Not only on the crown but also the roots, which are proportionally slender.

DISCUSSION

SYSTEMATICS OF THE FAMILY POLYDOLOPIDAE

The genera recognized in this work are *Antarctodolops*, *Amphidolops*, *Archaeodolops*, *Eudolops*, *Hypodolops*, *Kramadolops*, *Pliodolops*, *Pseudolops* and two undescribed genera (Gen. et sp. indet. 1; Gen. et sp. indet. 2). A list of genera and species can be found in Table 2.

Polydolops

Previous to this analysis, the genus *Polydolops* was diverse, being represented by different species. Some of them, with a few cusps in their molars (e.g. *P. thomasi*) and others with molars with crenulated edges and several cuspules united by their bases (e.g. *P. serra*). Therefore, when a new species was described, it usually was included in this genus (e.g. Tejedor *et al.*, 2009). The analysis shows that *Polydolops*, as previously conceived, is polyphyletic (Fig. 4), now only including the type species, *P. thomasi*.

Ameghino (1903) recognized the genus *Archaeodolops* to include the single species *A. clavulus*, previously assigned by him to *Polydolops* (Ameghino, 1902). Ameghino based this change on the consideration that *A. clavulus* was primitive because of, for example, the lack of serrations on the p3. These serrations were observed by Marshall (1982), who reassigned the species to *Polydolops*. In our analysis, the genus *Archeodolops* is revalidated, because it does not group with *Polydolops* but appears in a trichotomy with Gen et sp. indet. 1 and the clade grouping the remaining polydolopids.

The species '*Polydolops*' *serra*, '*Polydolops*' *rothi*, '*Polydolops*' *winecage* and '*Polydolops*' *kamektsen* are clustered together in node 11. Although they were all considered part of *Polydolops*, this analysis argues otherwise, thus confirming a different genus. *Pliodolops primulus* was a species recognized by Ameghino (1902), and now considered a synonym of '*Polydolops*' *serra*. In view of the results here presented, the genus *Pliodolops* is revalidated to include the species *Pliodolops primulus*, *P. rothi*, *P. winecage* and *P. kamektsen*.

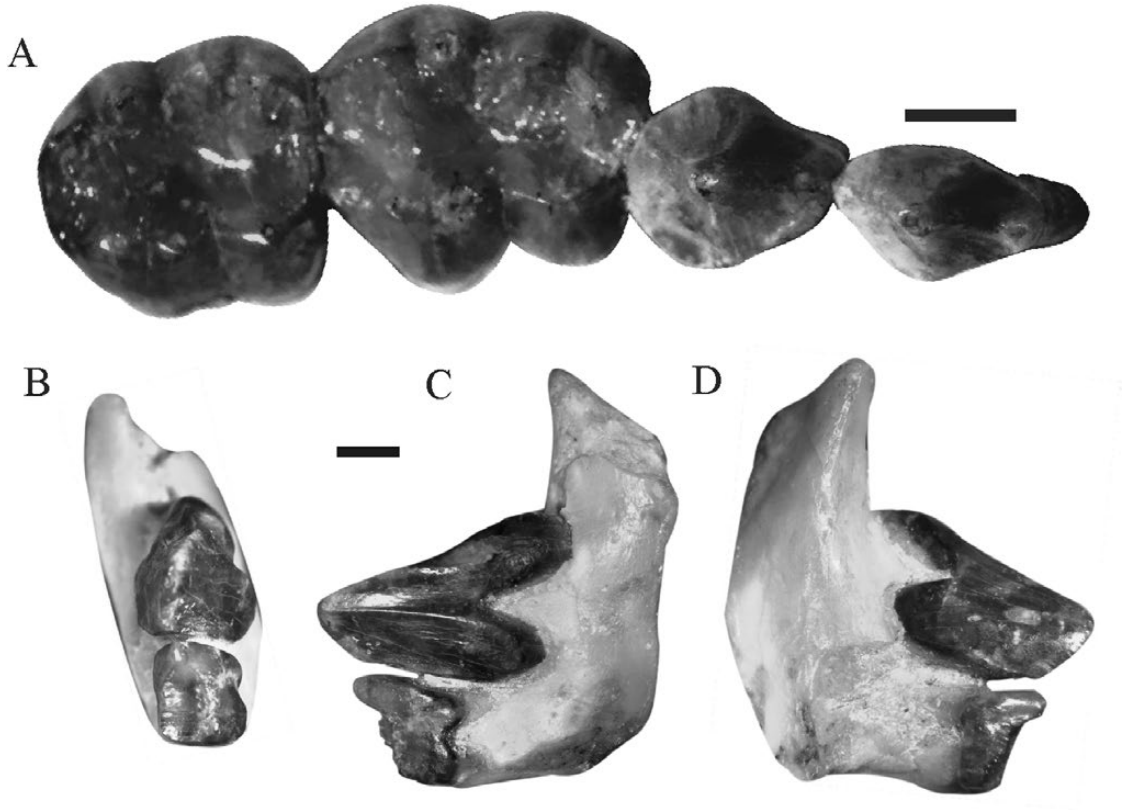

Figure 10. A, Gen. et sp. indet. 1. Right maxillary fragment with P2-M2 (MLP 77-VI-14–5) in occlusal view. B–D, Gen. et sp. indet 2. Left mandible with p3-m1 (LIEB-Pv 1178). B, occlusal view. C, labial view. D, lingual view. Scale bar = 2 mm.

The species recently recognized by Tejedor *et al.* (2009), '*Polydolops*' sp. nov. 1, 2 and 3 are not related to *Polydolops thomasi*. *Polydolops* sp. nov. 1 and 2 correspond to *Hypodolops sapoensis*, a species that forms a clade with *Antarctodolops*, *Amphidolops* and *Pliodolops*. '*Polydolops*' sp. nov. 3 (Gen. et sp. indet 2 in this work) cannot be assigned precisely.

Eudolops tetragonus and the genus Kramadolops

The genus *Kramadolops* was recognized by Goin *et al.* (2010) to include *K. abanicoi*, *K. mayoi* and *K. mckennai*. These species were first regard as pertaining to *Polydolops*. Goin *et al.* (2010) also recognized two new species from the Early Oligocene deposits of Patagonia: *K. fissuratus* and *K. maximus*. The genus was defined as follows: 'large size, molars subequal in length and width (i.e. they do not decrease rapidly in size from m1 to m3); upper molars without accessory labial cuspules; upper and lower molars (except m3) divided into two lobes (anterior and posterior) due to deep labial and lingual flexa/flexids; P2 considerably larger than P3; p3 large, with asymmetrical (in lateral view) anterior and posterior crests (the posterior crest is shorter and more horizontally set)' (Goin *et al.*, 2010: 86). In the phylogenetic analysis presented here, the genus *Kramadolops* is recovered as a monophyletic group, including all species previously assigned by Goin *et al.* (2010) plus *Kramadolops hernandezi* (Marshall, 1982).

Antarctodolops

Woodburne & Zinsmeister (1984) described *Antarctodolops dailyi* and compared it with *Kramadolops mayoi* (as *Polydolops mayoi*) mainly because of the temporal interpretation. They considered the Antarctic fauna as Eocene–Oligocene in Age (posterior dating gave that fauna an Early Eocene age; Chornogubsky *et al.*, 2009). In their comparison they found significant differences between both species, like the presence of more cuspidated crowns in the molars of *Antarctodolops dailyi*. Later, Case *et al.* (1988) described a P3 that they considered as belonging to a new species and genus: *Eurydolops seymourensis*. Goin & Candela (1995) considered both species as *Polydolops*, because the differences were not enough to recognize new genera (but see the discussion above). Chornogubsky *et al.* (2009) considered *Antarctodolops* as a valid genus and argued that its features were shared partly between

Table 2. Taxonomic list after the revision presented in this work

FAMILY POLYDOLOPIDAE Ameghino, 1897
Genus *Eudolops* Ameghino, 1897
E. tetragonus Ameghino, 1897
Genus *Archaeodolops* Ameghino, 1903
A. clavulus (Ameghino, 1902)
Genus *Polydolops* Ameghino, 1897
P. thomasi Ameghino, 1897
Genus *Kramadolops* Goin, Abello, & Chornogubsky, 2010
K. mayoi (Odreman Rivas, 1978)
K. abanicoi (Flynn & Wyss, 1999)
K. fissuratus Goin, Abello, & Chornogubsky, 2010
K. hernandezi (Marshall, 1982)
K. maximus Goin, Abello, & Chornogubsky, 2010
K. mckennai (Flynn y Wyss, 2004)
Genus *Hypodolops* nov.
Hypodolops sapoensis gen. et sp. nov.
Genus *Pseudolops* Ameghino, 1902
P. princeps Ameghino, 1902
Genus *Antarctodolops* Woodburne & Zinsmeister, 1984
A. dailyi Woodburne & Zinsmeister, 1984
A. mesetaense Chornogubsky, Goin, & Reguero, 2009
Genus *Amphidolops* Ameghino, 1902
A. serrula Ameghino, 1902
A. yapa (Simpson, 1935b)
A. minimus sp. nov
A. intermedius sp. nov
Genus *Pliodolops* Ameghino, 1902
P. primulus Ameghino, 1902
P. kamektsen (Simpson, 1935b)
P. rothi (Simpson, 1936)
P. winecage (Simpson, 1935b)
Genus et sp. indet. 1
Genus et sp. indet. 2

Amphidolops (e.g. wrinkled enamel, presence of several cusps) and *Polydolops* (e.g. presence of a large lingual cusp on the m1). They also considered *A. dailyi* and *E. seymourensis* as synonyms and described the new species *A. mesetaense*.

The analysis carried out in this work is concordant with the hypothesis of Chornogubsky *et al.* (2009). Moreover, it can be argued that this genus is related to the clade including *Amphidolops* plus *Pliodolops*. The latter including species formerly assigned to *Polydolops*. This relationship is consistent with the observation of *Antarctodolops* species having characters shared with both *Amphidolops* and *Polydolops* (here *Pliodolops*) as commented by Chornogubsky *et al.* (2009).

EVOLUTION AND EXTINCTION OF POLYDOLOPIDAE

Polydolopidae is a marsupial family whose biochron spans over 30 million years and includes most of the Palaeogene from southern South America and the Antarctic Peninsula. Its evolution included few records until Middle Eocene times, when they diversified. A rapid decline followed in the Early Oligocene.

The first record of a polydolopid occurred in Patagonia, where a rainforest-dominated palaeoflora was reported (Barreda & Palazzesi, 2007), which corresponds to *Amphidolops yapa* from the Late Danian strata of Cerro Redondo, Chubut Province, Argentina (Simpson, 1935b) (Fig. 11). This species, only represented by an isolated M3, shows derived features, such as a crenulated (wrinkled) enamel and subtriangular shape. A great time-lapse occurs until the next record of a polydolopid occurs (*P. kamektsen*; Cañadón Hondo; Chubut Province) in the *Kibenikhoria* fauna of Simpson (1935b; Itaboraian SALMA), and the diversification of the group occurred in the Late Palaeocene, when some of the clades appear to have originated (i.e. *Amphidolops* and *Pliodolops*). The Middle Eocene shows a diverse record, with several species recorded from Patagonia and the Antarctic Peninsula. Both regions, nearer to each other then their present-day location, had difference in their floras. In Patagonia, a Palaeoflora Mixta without *Nothofagus* Blume (Nothofagaceae) was typical (Troncoso & Romero, 1998). Moreover, the fossil floras near Laguna Fria (Paso del Sapo fauna) have a high plant diversity and represent diverse rainforests with Australasian components, including Podocarpaceae and ferns (Wilf *et al.*, 2005; Zamaloa *et al.*, 2006), but *Nothofagus* has not been reported from there yet [but see Wilf *et al.* (2005)]. In the Antarctic Peninsula, the palaeoflora suggests a temperate climate with abundant precipitation and marked seasonality (Case *et al.*, 1988; Gandolfo *et al.*, 1998), and even though it is dominated by Podocarpaceae, *Nothofagus* is widely represented (Pujana *et al.*, 2014).

Before Vacan times, all Polydolopidae were derived, multicuspid, crenulated forms, corresponding to the clade represented by Node 7: (*Hypodolops*, *Antarctodolops*, *Amphidolops* and *Pliodolops*) (Fig. 4). The Casamayoran is represented, except for a few exceptions (e.g. *A. serrula*), by simpler forms, less cuspidate and, in some cases, with no wrinkled enamel. The only polydolopids surely known on the Vacan subAge are *P. thomasi* and *P. primulus*. Most of the Casamayoran species were exhumed from Barrancan outcrops, thus being this subAge the one that presents the largest taxon richness. The Mustersan SALMA is characterized by *P. thomasi* and the first appearance

of a *Kramadolops*, *K. mayoi* (Odreman Rivas, 1978). The Middle to Late Eocene Patagonian landscapes are characterized by Palaeoflora Mixta with *Nothofagus*, and the progressive replacement of megathermal communities by meso- and microthermal rainforests (Barreda & Palazzesi, 2007). This was finally concluded in a typical Antarctic Palaeoflora at the beginning of the Oligocene (Troncoso & Romero, 1998; but see: Strömberg *et al.*, 2013), where the last polydolopids are recorded (all from the genus *Kramadolops*; Goin *et al.*, 2010) in the Tinguiririan faunas (and SALMA) of Argentina and Chile (Flynn & Wyss, 1999, 2004; Goin *et al.*, 2010) and the post-Tinguiririan La Cantera fauna (Goin *et al.*, 2010).

Several hypotheses have been argued about the extinction of polydolopids. Odreman Rivas (1978: 34) commented that they appeared as 'a rapidly specialized group, more specifically adapted and less tolerant in their ecological relationships' (in Spanish in the original). Their extinction must be related with the appearance of caviomorph rodents, that should have entered South America at that time (the author referred to the Late Eocene, Mustersan SALMA). Later, Marshall (1982) argued that the ecological role of the Polydolopidae in the Riochican and Casamayoran was occupied in the Oligocene and later by the paucituberculatans (abderitids and palaeothentids) and by caviomorph rodents and platyrrhine primates. Both Odreman Rivas (1978) and Marshall (1982) hypotheses propose competitive displacement as the more plausible cause of the extinction of the polydolopids. However, even though a great diversity of Paucituberculata occurs in the Miocene, they appeared as a group in the Early Eocene, and the palaeothentids and abderitids diversified during the Oligocene (Abello *et al.*, 2018), thus coexisting with the polydolopids for most of the Palaeogene. Even though some authors considered opportunistic replacement as plausible (Ortiz-Jaureguizar, 2003), more recently Abello *et al.* (2018) argued that the differences in body mass among the Abderitids (284–391 g) and the last polydolopids (3.5 kg) prevent the former from having competed with the latter.

About the ecological specificity that Odreman Rivas (1978) hypothesized for polydolopids, that could not be the case: the polydolopids evolved in tropical environments or regions with mixed Palaeoflora (e.g. *Carodnia* zone; Paso del Sapo locality; Troncoso & Romero, 1998; Tejedor *et al.*, 2009) but they were also recorded later from most temperate to cool climates (La Meseta Formation in Marambio Island, Antarctic Peninsula, Chornogubsky *et al.* 2009; La Cancha and La Cantera localities, Sarmiento Formation, Goin *et al.*, 2010). This could indicate a wider range of adaptability.

Finally, the earliest rodents were known from the Late Oligocene (Deseadan SALMA) when Marshall (1982) wrote his revision on the Polydolopidae. Since then, rodents from the Early Oligocene (Tinguiririan SALMA and post-Tinguiririan/pre-Deseadan fauna) were discovered in southern South America (Flynn *et al.*, 2003; Vucetich *et al.*, 2005), and even earlier, Middle Eocene rodents were recorded from Peru (Antoine *et al.*, 2012, 2016). Thus, it is evident that polydolopids coexisted some time with caviomorph rodents and the differences in body mass considered by Abello *et al.* (2018) for abderitids and polydolopids could also be observed among polydolopids and caviomorph rodents, thus permitting to arrive to similar conclusions about the implausibility of competitive displacement.

Pascual (1984) commented that episodes related with mammalian evolution are coincident with global events that generated environmental and climatic changes. Coinciding with him, Goin *et al.* (2010) hypothesized about the extinction and mammalian turnover during the Early Oligocene: the Patagonian hinge (occurred at the end of the Early South American phase and beginning of the Late South American phase *sensu* Goin *et al.*, 2012). At that time, a global cooling was taking place (Zachos *et al.*, 2001).

The opening of Drake Passage was critical to the formation of the Antarctic Circumpolar Current (and subsequent Antarctic ice sheets) and global cooling in the Middle of the Cenozoic (Livermore *et al.*, 2004). The presence of glaciers was observed in both East and West Antarctica at the Eocene–Oligocene boundary, even extending throughout the Antarctic Peninsula (Ivany *et al.*, 2006). Scher & Martin (2006) commented that the early opening of Drake Passage occurred over 41 Mya (shallow waters), intermediate depth occurred *c.* 37 Mya and deep-water circulation started 34 Mya. Later, Lagabrielle *et al.* (2009) inferred a strong Antarctic Circumpolar Current about 32 Mya. Thus, these changes could have been the main factors that led to the cooling that Southern South America suffered at the Eocene–Oligocene boundary (Livermore *et al.*, 2004).

As mentioned above, southern South America (e.g. Patagonia) has been affected by climatic deterioration and the cooling of the region evidenced by the floristic changes from a Mixed Palaeoflora with *Nothofagus* (e.g. lower Nirihuau; Troncoso & Romero, 1998) to an Antarctic Palaeoflora (e.g. middle Nirihuau; Troncoso & Romero, 1998) in northern Patagonia. In turn, towards the Eocene–Oligocene boundary the precipitations show an important decrease (Hinojosa, 2005). This was also shown by the disappearing of the order Zingiberales, plants that imply relatively warm moist habitats even though few open habitats were significant until later in the Oligocene (Strömberg *et al.*, 2013). This means that,

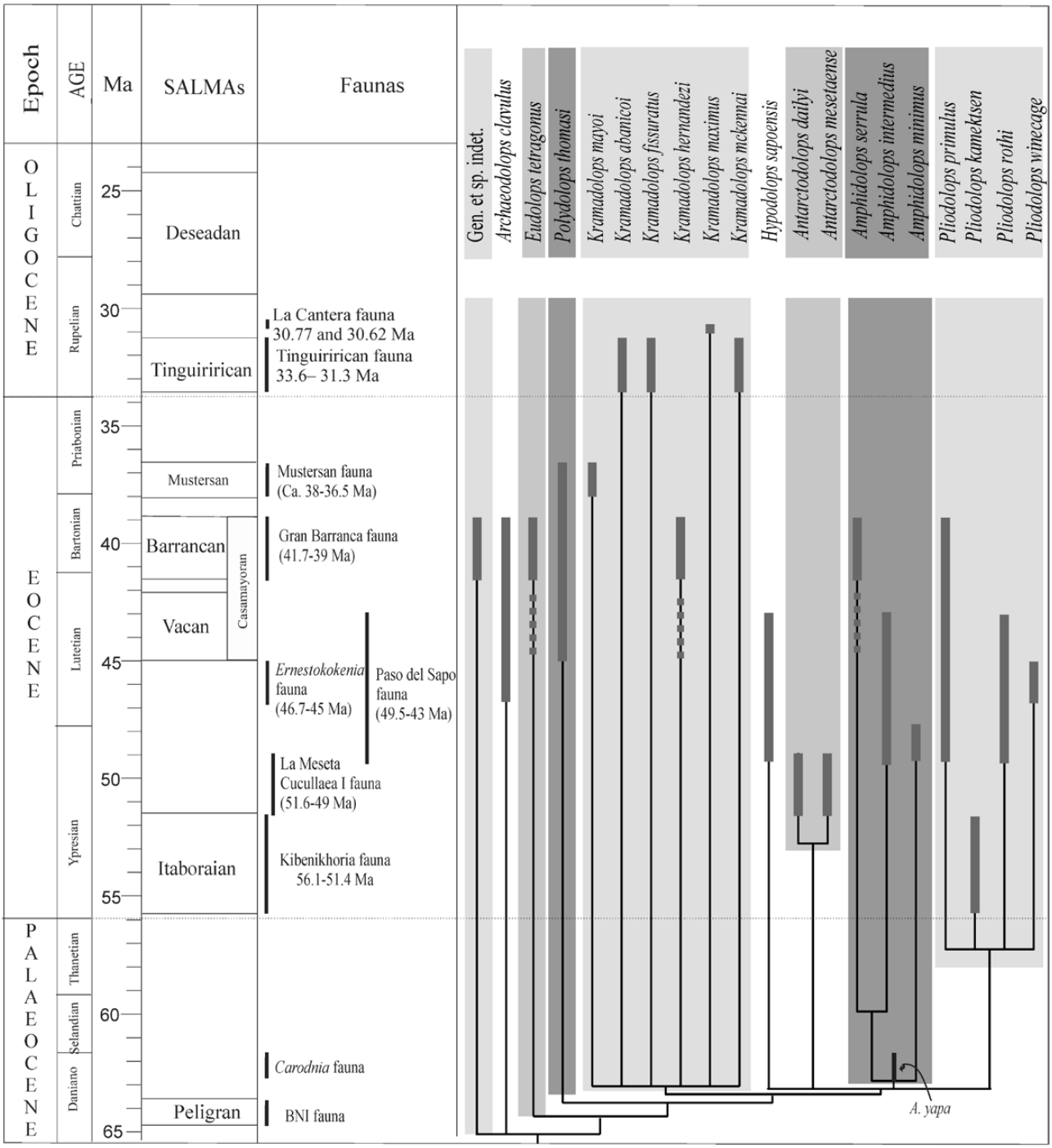

Figure 11. Time-calibrated cladogram of Polydolopidae based on relationships recovered from the strict consensus based on relationships recoveres from the strict consensus and the addition of *Amphidolops yapa*. Heavy lines correspond to the known temporal range. Dotted lines correspond to possible temporal range. Geochronological units, SALMAs/faunas as in Figure 2.

since the Early Palaeocene, the climate in southern South America was turning from more uniform conditions (megathermal rainforests; Wilf *et al.*, 2013) to cooler and more seasonal and dry conditions (Ortiz-Jaureguizar & Cladera, 2006; Barreda & Palazzesi, 2007).

In their analysis of the fauna from Tinguiririca (Chile), Flynn *et al.* (2003) argued that the most

important palaeoecological turnover in South America occurred between Mustersan and Tinguiririan SALMAs. This was further argued by Goin *et al.* (2010) who hypothesized that the La Cancha association (Early Oligocene, Tinguiririan SALMA from Chubut Province) reflects the cooling already initiated by the tectonic and oceanic events mentioned above. Observing the marsupial faunas from the Early Oligocene (La Cancha and La Cantera localities, in Chubut Province), they suggested that at this moment occurred the larger faunal turnover of the Cenozoic from the Southern Hemisphere. This episode suggests that the mean global temperature could have unchained the marsupial faunal turnover, resulting in the radiation of many groups and the extinction of others.

The metatherian associations from La Cancha and La Cantera represent, both taxonomically and ecologically, strong differences when compared with other Palaeogene faunas. Throughout this temporal span there are the last representatives of Caroloameghinidae, Sternbergiid 'Didelphimorphia' and the Polydolopimorphia Hatcheriformes and Polydolopiformes. Some taxa make their first appearance as well, as the Bonapartheriiformes Argyrolagids, the Paucituberculata quickly radiates, with representatives of Pichipilidae and Palaeothentidae. Finally, in La Cantera fauna appear modern and larger Borhyaenids (Goin *et al.*, 2010).

Palaeocene and Eocene marsupial faunas are characterized mainly by granivores, omnivores and insectivores, while many Oligocene marsupials show adaptations for more herbivorous and granivorous diets. The morphology of the molar crowns from several Oligocene marsupials from Patagonia is suitable for more abrasive diets (e.g. unilateral hypsotodonty) (Goin *et al.*, 2010). Goin *et al.* (2010) considered several hypotheses about the turnover: (1) the origin of Metatherians was catalysed by the beginning of the 'Greenhouse World' in the Cretaceous period; (2) the South American, Antarctic and Australian radiations had their climax at the Eocene climatic optimum; (3) the *Bisagra Patagonica* event implies, at least for South American marsupials, a change in their diets and adaptive niches that, for eutherian mammals, are correlated with lower basal metabolic rates (i.e. herbivory, carnivory).

The exposed above is relevant to the study of the evolution within Polydolopidae because the climatic deterioration and evolutionary patterns among most Metatherians could also explain the changes in diversity and evolution of the Polydolopidae. Derived forms are already present in Early Palaeocene strata, thus suggesting an Early Palaeocene or even a Cretaceous origin for the Polydolopidae (Chornogubsky *et al.*, 2009). On the other hand, a stark decrease of polydolopid species can be seen in Late Eocene–Early Oligocene times, with the last polydolopid, *Kramadolops maximus*, recorded in post-Tinguiririan–pre-Deseadan rocks from Chubut Province (Goin *et al.*, 2010).

An apparent contradiction appears when arguing that polydolopids could not adapt to the great decrease of the temperature and floristic turnover that took place in the Early Oligocene but that they had been adapted to similar conditions in the Middle Eocene from Antarctica. It could be considered that Antarctic polydolopids, resistant to cooler environments, pertained to different clades than *Kramadolops*. However, it is interesting to note that, even though the environments seem similar, they had vast differences (see above). Birney & Monjeau (2003) studied the distribution of living South American marsupials, and they determined that the southernmost distribution of the group is related to the mean minimum extreme temperature. This is related to the low basal metabolic rate that occurs in marsupials. Martin (2008), studying the living marsupials from Patagonia, argued that regionally, the precipitation are the ones that limit the distribution of the species, even though they live in different environments. These considerations could also explain the observations about the decrease in the diversity of polydolopids, related probably to the deterioration of the climate in Patagonia (cooling and drying of the environments during the Oligocene), that may have had an important role in the extinction of the group.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Appendix S1. Character list.
Figure S1. Outline drawings of mandibular fragments showing the height of the mandible at the diastema. A. Equal to the one at the level of the molar row. B. Considerably lower than the high at the molar row.
Figure S2. Outline drawings of p3 in labial view. A. Asymmetrical type, with one labial rib. B. Asymmetrical type, with two labial ribs. C. Symmetrical type, with one labial rib.
Figure S3. Outline drawing of m1 of different Polydolopimorphia showing the cusps of the trigonid. A. *Roberthoffstetteria nationalgeographica*. B. *Epidolops didelphoides*. C. A *Antarctodolops dailyi*.
Figure S4. Lower m1 outline drawing from Polydolopids. A. m1 with hypoconid more anteriorly oriented and with a cuspule anterior to the protoconid. B. m1 with hypoconid aligned with the entoconid and large lingual cusp in the talonid.
Figure S5. Lower m2 outline drawings showing the presence of accessory cusps and the position of the paraconid in Polydolopiformes. A. *Roberthoffstetteria*. B. *Polydolops*. C. *Kramadolops*.
Figure S6. Outline drawings of an m1 of a Polydolopid showing the difference in height on the labial and lingual margins. A. Labial view. B. Lingual view.
Figure S7. Outline drawings of an m2 of polydolopids showing the difference in the position of the hypoconid. A. Hypoconid more anteriorly positioned than the entoconid. B. Hypoconid and entoconid aligned. Dotted line shows the position of the hypoconid.
Figure S8. Outline drawings of different types of P3. A, *Antarctodolops* type (symmetric). B. *Kramadolops* type (asymmetric). Both in labial view.
Figure S9. Outline drawings of M1 from Polydolopimorphia in occlusal view. A. *Roberthoffstetteria*. B. *Bonapartherium*. C. *Antarctodolops*.
Figure S10. Outline drawings of M1 from Polydolopiformes. A. *Roberthoffstetteria*. B. *Pliodolops*. C. *Amphidolops*.
Figure S11. Outline drawings of M1 in occlusal view. A. With no lingual accessory cusps. B. With one accessory cusp in the anterior lingual lobe. C. With several accessory cusps on the posterior lingual lobe.
Figure S12. Outline drawings of M2 in occlusal view. A. *Roberthoffstetteria nationalgeographica*. B. *Pliodolops primulus*. C. *Pliodolops rothi*.
Appendix S2. Character matrix.
Appendix S3. List of synapomorphies.
Appendix S4. Measurement tables.